University of Alberta

Relating rarity and phylogeny to the autecology of mosses: A comparative study of three rare-common species pairs in the Front Ranges of Alberta, Canada.

by

Natalie Laura Cleavitt ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Relating rarity and phylogeny to the autecology of mosses: A comparative study of three rare-common species pairs in the Front Ranges of Alberta, Canada submitted by Natalie Laura Cleavitt in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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The Road goes ever on and on
Down from the door where it began
Now far ahead the Road has gone,
And I must follow if I can
Pursuing it with eager feet
Until it joins some larger way
Where many paths and errands meet
And whither then? I cannot say . . .

The Old Hobbit Walking Song
J.R.R. Tolkien

To the mosses of the mountains
Who lured me here,
Forebore my inquiries,
And deepened my understanding.
May this benefit you in some small way.

ABSTRACT

Rare species may have ecological characteristics in common that either as a result of or in response to their restricted distributions. These similarities are most soundly documented through autecological comparisons based on closely related rare-common species pairs that control for phylogeny. In this thesis, three rare species, *Mielichhoferia macrocarpa*, *Didymodon johansenii*, *Mnium arizonicum*, and three common species, *Bryum pseudotriquetrum*, *D. rigidulus*, *M. spinulosum*, respectively matched, were compared by assessments of habitat specificity, establishment ability, stress tolerance, propagule viability, colony demography, influence of disturbance regime and frequency of neighbor contact. In general, ecological differences between rare and common species were found, and in an analysis of ecological traits pertaining to local persistence the rare species clustered together. Two of the rare species most similar to each other, *M. macrocarpa* and *D. johansenii*, were restricted during the establishment stage, and these two species have similar widely disjunct distributions. In contrast, *M. arizonicum* is endemic to North America and ecologically very similar to its common congener. *Mnium arizonicum* was concluded to have the physiological ability to expand its range in the establishment and adult stages, and may be dispersal limited. Two common species had clear physiological limitations mainly in the adult stage, and the third, *D. rigidulus*, was limited during the establishment stage. As with *M. macrocarpa* and *D. johansenii,* this establishment restriction corresponded to substrate specificity confirming the link between these two factors in mosses. Physiological substrate restrictions were documented for *M. macrocarpa* and *D. rigidulus*, species found on substrates with high pH and low organic matter, while *D. johansenii* was physically limited by disturbance. The effect of habitat disturbance regimes varied between establishing propagules and established colonies. Species with lower colony disturbance tended to have more frequent neighbor encounters as predicted by plant strategy theory. Propagule viability did not relate to establishment ability suggesting that dispersal and establishment are functionally separate in mosses and should be treated separately in metapopulation models. The complexity of mechanisms responsible for habitat specificity and narrow realized niches shown here agrees with predictions of several rarity hypotheses and, more importantly, demonstrates the necessity of empirical studies to test these hypotheses.

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Table of contents

Page #

Chapter 1: General Introduction to rarity theory- does it apply to plants and how fully has it been tested? **1**
- *Rarity definitions and terminology.* *2*
- *Patterns in rarity.* *7*
- *Rarity in theory.* *12*
- *Autecological plant studies.* *15*
- *Rarity in Bryophyta: comparison to vascular plants.* *18*
  - *Dispersal.* *18*
  - *Reproductive biology.* *19*
  - *Disturbance regime.* *21*
  - *Establishment ability.* *22*
  - *Competition.* *22*
  - *Habitat specificity.* *23*
  - *Historical climate change.* *24*
  - *Herbivory.* *24*
- *Evaluation of current rarity theory.* *24*
- *Thesis framework of limiting factors.* *25*
- *Conclusion.* *29*
- **Literature cited** **30**

Chapter 2: Study species synopsis- how do my species differ and are my rare species typical? **60**
- *Geographic distributions of species pairs.* *64*
- *Research study sites.* *67*
- *Local abundance of study species.* *77*
- *Habitat specificity of species pairs.* *81*
  - *General habitat descriptions.* *81*
  - *Habitat measurements at study sites.* *83*

Chapter 2 continued **Page #**

Species in relation to rare-common categories. *89*

Reproductive potential. *92*

Sexual reproductive potential. *94*

Asexual reproductive potential. *97*

Reproduction and rarity. *99*

Conclusions. *100*

Literature Cited **101**

Chapter 3: The role of physiologically based substrate specificity for six species occurring on substrates with varying pH and percent organic matter **108**

METHODS 112

Study species. *112*

Substrate organic matter and pH measurements. *113*

Substrate short-term establishment experiment. *113*

RESULTS 115

Substrate breadths. *115*

Substrate preferences and establishment ability. *115*

Rare and calcicole and substrate sensitivity. *121*

DISCUSSION 121

Substrate breadths. *121*

Substrate preferences and establishment ability. *122*

Rare species' substrate sensitivity. *122*

Calcicole species substrate sensitivity. *123*

Conclusion. *124*

Literature Cited **126**

Chapter 4: A test of physical limitation to specific substrates during establishment for *Didymodon johansenii*, a rare moss. **Page #** **131**

METHODS 134

Species taxonomy & recognition. 134

Log characterization. 134

Measurement of log environment. 137

Regeneration experiment. 139

RESULTS 141

DISCUSSION 146

Log suitability. 146

Didymodon johansenii regeneration. 152

Conclusion. 153

Literature Cited 154

Chapter 5: Physiological tolerance of six moss species as colonies and fragments measured by exposure to short- and long-term stress 160

METHODS 163

Study species and sites. 163

Characterization of colony environments. 166

Moisture. 166

Light. 166

Short-term stress responses of colonies & gametophyte fragments. 167

Chlorophyll fluorescence. 167

Light response curves. 169

Desiccation tolerance. 170

Long-term stress response of colonies and gametophyte fragments. 172

Reproduction comparison. 174

Sexual reproduction allocation. 174

Vegetative propagule regeneration. 174

Species establishment plot details 175

Chapter 5 continued **Page #**

RESULTS 176

Characterization of colony environments. *176*

Short-term stress responses. *176*

Long-term stress response. *180*

Reproduction comparison. *187*

DISCUSSION 191

Adult physiology and habitat characteristics. *191*

Propagule physiology, adult habitat characteristics and potential dispersal vectors. *194*

Concurrence of stress responses. *196*

Propagule viability and reproductive strategy. *196*

Conclusion. *198*

Literature Cited **199**

Chapter 6: Local persistence of three rare and three common moss species explored through establishment experiments, reciprocal transplants, and colony mapping **214**

METHODS 216

Study species & sites. *216*

Establishment ability. *217*

Species details. *218*

Colony growth and disturbance. *220*

Reciprocal colony transplants. *222*

Colony neighbor interaction. *223*

RESULTS 224

Establishment ability. *224*

Colony growth and transplantation effects. *232*

Colony disappearance and neighbor contact. *236*

DISCUSSION 240

Chapter 6 continued **Page #**

DISCUSSION 240

Comparison of species limitations. *240*

Comparison to existing hypotheses. *244*

Conclusion. *248*

Literature Cited **249**

Chapter 7: Synthesis: does the autecology of six moss species reflect rarity or phylogeny? **258**

Analysis of ecological similarity and trait occurrence. *259*

Ecological similarity. *261*

Co-occurrence of ecological traits. *266*

Literature Cited **272**

Chapter 8: General discussion and conclusions. **277**

Literature Cited **282**

Appendix A: Summary of autecological studies on rare vascular species used in literature review in Chapter 1. **285**

Appendix B: Ecological character state scores for summarizing co-occurrence of traits by rarity and phylogeny in Chapter 7. **293**

List of Tables

Page #

Table 1.1. The four most common species distribution patterns and their relationship to terminology that has been used to describe them at varying spatial scales. The numbers correspons to categories depicted in Figure 1.1a. 3

Table 1.2. Early ideas concerning plant rarity and conclusions for rare plant limitations summarized from the review of Fiedler (1986). 8

Table 1.3. Summary of recent approaches to outlining patterns in rarity. The aproach names as given by the authors are in bold. Fiedler & Ahouse (1992) suggest traits of species that need to be considered when exploring the causes of rarity. Rosenweig & Lomolino (1997) outline traits that pre-dispose species to rarity. Gaston & Kunin (1997) synthesize traits associated with rare species without implying whether they are a cause or consequence of rarity. 10

Table 1.4. Current biological theories that have been proposed to explain positive interspecific abundance-range size relationships (based on Gaston *et al.* 1997) and their implications/ predictions for rare species relative to common species. Theory numbers correspond to Tables 1.5 and 1.6. Range position is not considered further and so is not numbered here (see text for more detail). 14

Table 1.5. Literature review of autecological studies on rare vascualr plant species. The table summarizes results for 130 species from 149 studies summarized in more detail in Appendix A. Relevant theory refers to rarity theories by their numbering in Table 1.4. Here the number of species considered for a limitation and the number that were limited by that factor are presented. There were eight main limitating factors found for vascular plants. The limitation numbers given here are also used in Appendix A. For several categories there was a more specific limitation stated and the number of species with the specific limitation are given in parentheses beside the totals. 17

Table 1.6. Summary of studies on rare species in which the data and/or stated conclusions pertain to recent theories explaining rarity. Predictions for rare species by each of these theories are outlined in Table 1.4. Studies from the bryophyte literature are in italics. Both synthetic and empirical papers are included here. Synthetic studies are in bold. Metapopulation dynamics theory requires documentation of both dispersal limitation and lower population growth rates (Table 1.4) and none of the reviewed studies include both of these measurements. 26

Table 2.1. Species names, abbreviations and general morphological comparison of plant size and colony habit. Values are compiled from Crum & Anderson (1981) and Lawton (1971) for *B. pseudotriquetrum* and *M. spinulosum*, Lawton (1971) for *M. macrocarpa*, *D. johansenii* and *M. arizonicum*, and Zander (1981) for *D. rigidulus* var. *gracilis*. Rare species are bolded. 61

Table 2.2. Reference table of study species occurrence in Alberta and North America and globally. Rare species are in bold typeface immediately before their species pair. Ranks are assigned relative only to the other study species and are meant to illustrate rather than quantify differences between species. Ranks are relative to the study species and were assigned with 1 = smallest distribution. For sum of ranks, the lowest possible score is 2 and the highest is 11.5. 65

Table 2.3. Reference table of study sites summarizing map reference number for Figures 2.3-4, site location, elevation, and studies conducted at the site. The abbreviations used for studies conducted at each site followed by the chapters where the studies are presented are as follows: M = colony assessments by mapping (2,6), C = neighbor contact assessment (2,6), H = habitat quantification: pH, % OM, temperature & light (2,3,4,5), W = moisture quantification (2,3,4,5), EA = establishment and adult transplant experiments (6), F = *in situ* chlorophyll-fluorescence comparisons (6), SE = silt experiment (4). 68

Table 2.4. Climate normals from four recording stations in the study area. Data are from the Canadian climate normals 1961-1990 (Environment Canada 1998). 76

Table 2.5. Summary of study species' local abundance based on colony area, density and site area. Mean percent cover is calculated by mean colony area and density (i.e., mean area required to encounter 50 colonies). Rare species abbreviations are in bold. The overall rank is based on mean percent cover at a site where 1 = least abundant and 6 = most abundant. 78

Table 2.6. Qualitative habitat specificity of six study species from literature reports and field observations. Rare species abbreviations are in bold. For the rank sum the lowest possible rank is 2 and the highest is 12. 82

Table 2.7. Statistics of standardized PCA analysis of species sites in environmental space shown in Figure 2.5. Only five of the six environmental variables were correlated to the significant axes of the ordination, therefore rainfall is not included here. 86

Table 2.8. Habitat parameters measured in 1998 growing season for six moss species. 88

Table 2.9. Summary of sexual reproduction in six study species. Sporophyte production descriptions specific to the study area are in bold. Rankings are given for sporophyte frequency throughout the species range and frequency within the study area is given in parentheses. Data for sporophyte frequency comes from 50 mapped colonies at 3 sites for each species. Mean spore size and seta length are from Crum & Anderson (1981) for *B. pseudotriquetrum*, *D. rigidulus* and *M. spinulosum* and from Lawton (1971) for *M. macrocarpa*, *D. johansenii* and *M. arizonicum*. 95

Table 2.10. Summary of asexual reproduction in six study species including developmental processes, asexual reproduction specialization and mean percent establishment of fragments in control plots from the field and growth chamber. Standard deviations are given in parentheses beside the mean. Percent regeneration measurements from the field are from 5 sites with 3 replicates each and the chamber experiment had 5 replicates on natural substrate. 98

Table 3.1. Summary of species establishment shown in Figures 3.3 and 3.4. Actual proportions of fragments alive with growth are shown in Figure 3.3 and the proportion of fragments with sprouts is shown in Figure 3.4. This summary is based on homogeneous subsets from Tukey HSD post-hoc analysis with species having the lowest proportion of fragments alive or sprouting designated by "a". Species abbreviations are the first letter of the genus and first three letters of the specific epithet. Homogeneous subsets (i.e., subsets composed of species for which there was no significant difference in establishment) are denoted by species that share the same letters. Species are listed in order of increasing regeneration. Rare species are indicated by bold typeface. 120

Table 4.1. Logistic regression model relating log variables to *D. johansenii* occurrence. 143

Table 4.2. Results of ANOVA for three environmental variables measured at three sites with seven logs classified as suitable and seven as unsuitable for *D. johansenii* habitat. F-values and their significance are shown. Significance values: ns = not significant at p=0.05, * p<0.05, ** p<0.01, *** p<0.001. 144

Table 4.3. ANOVA of found and live fragments at three sites on suitable and unsuitable logs and plots with and without silt (model d.f. = 83). Significance values: ns = not significant at p=0.05, * p<0.05, ** p<0.01, *** p<0.001. 148

Table 4.4. Log linear analysis of number of sprouting fragments. Final model: Sprout = Site + Suitability + Silt + Live + offset (sprouts/live). The null model deviance was 98.394 on 70 degrees of freedom and the final model residual deviance was 43.281 on 66 degrees of freedom. For variable deviance explained an * indicates significance at $\alpha = 0.05$ on χ^2 distribution with 1 degree of freedom. 149

Table 5.1. Comparison of 95% confidence intervals for slopes of ϕPSII and qN responses to increasing light intensity shown in Figure 5.4 for six moss species. For the regression analysis light intensity values were log transformed to linearize the variable relationships. Slopes with non-overlapping confidence intervals were considered statistically different at $\alpha = 0.05$. *Mnium spinulosum* is the only species differing in it's response to high light intensities. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species are in bold typeface. 178

Table 5.2. Coefficients and 95% confidence limits of equation parameters and coefficients of variation (r^2) for a non-linear regression model comparing recovery of yield after rehydration for six moss species (Fig. 5.5). The curve equation was:

$$\text{Yield} = \frac{(\text{A*time})}{(\text{B+time})}$$

where yield is effective quantum yield of photosystem II, A is the asymptote, time is time after rehydration in minutes, and B is the value of x when y = A/2. The asymptote here reflects completeness of yield recovery while B represents the time required for reaching half of the recovery yield. Parameters whose 95% confidence intervals do not overlap are considered significantly different at $\alpha = 0.05$. 181

Table 5.3. Difference between yield of dehydrated samples and yield of control samples 48 hours after rehydration of the treatment samples. Significance levels are from separate one-way ANOVA comparison of yield by species and significance levels were adjusted for multiple comparisons with ^{ns} $p > 0.008$, not significant and * $p < 0.008$. 183

Table 5.4. ANOVA comparison of photosynthetic yield recovery 24 hours after sample rehydration between two experiments in which the same four species were desiccated as whole colonies or gametophyte fragments. Plant material was collected from the same study sites for the two experiments. Model $r^2 = 0.858$. Significance levels for F value: ^{ns} $p > 0.05$, not significant and *** $p < 0.001$. 184

Table 5.5. Effects of storage condition and time on fragment viability for six moss species by three-way ANOVA. (ANOVA model df = 144, $r^2 = 0.914$.). The significance of p-values was confirmed by a randomization test using 30,000 iterations. See Methods for details. 185

Table 5.6. ANOVA comparison of fragment viability in two experiments where four moss species were stored for four months under dry conditions as fragments in the field or as colonies indoors. The indoor location had less variable overall environment and lower light levels than field location. 188

Table 5.7. Differences in species sexual reproductive allocation as expressed by sporophyte production. Field data were gathered from 150 colonies per species within the study area, each scored for the presence/absence of sporophytes. All herbarium specimens in ALTA (University of Alberta) for each species were also examined for presence/absence of sporophytes. Proportions that were not significantly different at $\alpha = 0.05$ in a Tukey-type multiple comparison test have the same letter superscript. 189

Table 5.8. Fragment regeneration potential under field and chamber conditions for six moss species. All species were planted in 1998; however, missing data signify that the majority of plots for that year were lost to disturbance. Species means that are significantly different between species within a column at $\alpha = 0.0125$ using Tukey Post-hoc have different superscript letters. For field data, mean fragment regeneration (three plots per site) at the same five replicate sites per species are reported. Chamber data are the means of five replicates from controls of data presented in Cleavitt (2001). 190

Table 6.1. Outline of establishment plot methodology by species and treatment. Reasons for changes in methodology are discussed in the methods section of this chapter and chapter 5. Methodology for *M. arizonicum* and *M. spinulosum* remained unchanged and these two species are not included here. *M. macrocarpa*, *B. pseudotriquetrum*, *D. johansenii* and *D. rigidulus* are abbreviated by the first letter of their genus and first three letters of their specific epithet. The rare species are in bold. 219

Table 6.2. Effect of species and site on fragment regeneration and recapture. Two-way ANOVAs by species pair on the proportion of fragments alive out of those planted and the number of fragments found out of those planted (for all balanced models $df = 60$). Variation in degrees of freedom reflects unbalanced models resulting from plot disturbance. Significance of F-values, ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and for values close to $p = 0.05$ the actual p-value is given as a superscript. Significant site by species interactions may represent the effect of native versus non-native sites on establishment and this *a priori* hypothesis was explored using planned comparisons (see text). 228

Table 6.3. ANOVA analysis of fragment regeneration for two species of *Mnium* at native and non-native sites when grown in plots alone and with the species pair as neighbor from May 1999 – August 2000. Significance of F-values: ns, $p > 0.05$, *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. Model $df = 120$ with 1 df for model intercept in GLM. 229

Table 6.4. ANOVA of fragment regeneration for *M. macrocarpa* and *B. pseudotriquetrum* in 1999 at *M. macrocarpa* sites after four months growing alone versus mixed together. Significance of F-values, ns, not significant, * < 0.05, ** < 0.01, *** < 0.001. Tukey HSD post-hoc multiple comparison test ($\alpha = 0.05$) was used to determine mean separation of sites. 231

Table 6.5. Chi-square analysis on counts of transplant survival for *M. macrocarpa*, *B. pseudotriquetrum*, *D. johansenii* and *D. rigidulus*. 235

Table 6.6. Colony size differences by frequency of neighbor encounters and losses to neighboring species. 241

Table 6.7. Summary of experimental results from this study with relation to relevant theory predictions. Symbols in support column are: ±, conflicting results, +, weak support, ++ support. 245

Table 7.1. Ecological characters scored for six study species summarizing the traits, their character states, and the chapter source for the data. Species scorings are given in Appendix B. 262

Table 7.2. Comparison of species similarity by number of shared traits out of fourteen scored (below diagonal) and Euclidean distance matrix for nine continuous traits relating to local persistence (above diagonal). Co-occurrence of scored traits are shown in Figures 7.2-4, and a dendrogram summarizing species similarity in traits relating to local persistence is shown in Figure 7.5. 265

Table A.1. Autecological studies on rare plant species summarized for species limitations. Studies are arranged alphabetically by family, genus and species. Names of species considered rare in the study are bolded. Range description for the species gives a proxy of rarity type. Methods used in the articles are abbreviated: environmental measurements (env), experimental (exp), monitoring (mon), survey (sur), and review (rev). Limitations considered and found are numbered to coincide with Table 1.5: 1. historical, 2. disturbance, 3. dispersal, 4. establishment, 5. competition, 6. differential mortality, 7.reproductive biology, and 8. habitat specificity. Studies where considered limitations are not stated are entered as "none". Likewise, studies where no limitation was found are entered as "none". Limitations that were mentioned, but were not addressed in the results of the paper are not included. Citations for studies that compared rare and common species are in bold. For species with more than one study, the studies were separated when they had been conducted by different authors on different populations of the species. References for this table are included in the literature cited section for Chapter 1. 285

Table B.1. Character state scores for fourteen ecological characters described in Table 7.1 that were used to map character states onto a dendrogram representing the evolutionary relationship of the six study species based on relationships within the Bryales (Vitt 1984) (Figs. 7.2-4). 293

List of Figure Legends

Page #

Figure 1.1. Two possible hypotheses on the relationship between species range size and local abundance: **a**. four distinct categories of the CURS model suggested by Söderström (1989), refer to Table 1.1, and **b**.continuous, positive linear relationship supported by Gaston (1996). 4

Figure 1.2. Conceptual models of how limiting factors might interact to influence species distribution: **a**. hierarchical and **b**. interactive. 28

Figure 2.1. Habit sketches of one plant for each study species showing morphological differences. The scale bar is 0.4 cm for all three pairs. The rare species are on the left with their names bolded. 63

Figure 2.2. Map of study region showing location of study area in Alberta (inset) and two main areas of study in the front ranges of the Rocky Mountains. The area containing Cadomin is enlarged in Figure 2.3 and includes sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum*. The area encompassing Devona Flats is enlarged in Figure 2.4 and includes sites for *D. johansenii*, *D. rigidulus* var. *gracilis*, and *M. spinulosum*. 73

Figure 2.3. Map of sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum*. Site numbers correspond to map #'s in Table 2.3. *Mielichhoferia* sites are numbers 1-6. *Bryum* sites are numbers 7-12, and *M. arizonicum* sites are numbers 29-33. 74

Figure 2.4. Map of sites for *D. johansenii*, *D. rigidulus* var. *gracilis*, and *M. spinulosum*. Site numbers correspond to map #'s in Table 2.3. *Didymodon johansenii* sites are numbers 13-22. *Didymodon rigidulus* var. *gracilis* sites are numbers 23-28. *Mnium spinulosum* sites are numbers 34-38. Light gray area marks Jasper National Park. 75

Figure 2.5. Standardized PCA ordination of five habitat parameters for the six study species sites showing the first two axes. Substrate pH, percent organic matter, light and temperature are all correlated to Axis 1 and Axis 2 represents moisture gradient. Site symbols are species specific: ● *M. macrocarpa*,○ *B. pseudotriquetrum*, ■ *D. johansenii*,□ *D. rigidulus* var. *gracilis*, ▲ *M. arizonicum*, and △ *M. spinulosum*. Numbers given beside the species symbols correspond to site names given in Table 2.3. 85

Figure 2.6. Study species classification by geographic range size and local abundance. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are in bold typeface. 90

Figure 2.7. Study species classification into the eight categories of Rabinowitz (1981) based on geographic range, local abundance and habitat specificity. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are bolded. 91

Figure 2.8. Position of six moss species along a rare-common gradient, see text for scoring details. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are in bold typeface. 93

Figure 3.1. Box plot of substrate organic matter content for six moss species from Canadian Rocky Mountain study sites in Alberta. Species pairs are bounded by brackets (see text for pair details) and common species have shaded boxes. Species' abbreviations are the first letter of the genus and first three letters of the specific epithet. The numbers of sites sampled for each species are given directly below the species abbreviation. Matching lower case letters denote homogeneous subsets from STP post-hoc analysis of Kruskal-Wallis test. Horizontal line represents the median value while the box around it shows the spread of 50% of the data. Vertical bars from the box give the interquartile range (80 % of the data). Circles indicate outliers (data values beyond 3 interquartiles). Asterisks denote extreme values. 116

Figure 3.2. Box plot of substrate pH-$CaCl_2$ values for six moss species from northern Rocky Mountain study sites in Alberta. Species pairs are bounded by brackets (see text for pair details) and common species have shaded boxes. Species' abbreviations are the first letter of the genus and first three letters of the specific epithet. The numbers of sites sampled for each species are given directly below the species abbreviation. Matching lower case letters abbreviations denote homogeneous subsets from STP post-hoc analysis of Kruskal-Wallis test. For explanation of box plot refer to Figure 3.1. 117

Figure 3.3. Comparison of species overall regeneration on control and treatment substrates. Species' abbreviations are the first letter of the genus and the first three letters of the specific epithet. Control substrates are species native substrates and are indicated by pair symbols in black (rare species) and white (common species). Treatment substrate is a substrate with the opposite extreme of pH and percent organic matter (see test for further details). Error bars represent one standard deviation. The significance of treatment effect by one-way ANOVA is indicated by: ns, $p>0.05$, *, $p<0.05$, **, $p<0.01$, ***, $p < 0.001$. 118

Figure 3.4. Comparison of species regeneration by sprouting on control and treatment substrates. Species' abbreviations are the first letter of the genus and the first three letters of the specific epithet. Control substrates are species native substrates and are indicated by pair symbols in black (rare species) and white (common species). Treatment substrate is a substrate with the opposite extreme of pH and percent organic matter (see test for further details). Error bars represent one standard deviation. The significance of treatment effect by one-way ANOVA is indicated by: ns, $p>0.05$, *, $p<0.05$, **, $p<0.01$, ***, $p < 0.001$. 119

Figure 4.1. Illustrations of the study species and experimental design. a. One stem of *Didymodon johansenii* that displays swollen leaf tips, leaves that have lost their tips, and general leaf habit when hydrated. b. Experimental design for regeneration experiment showing one log with three sets of plots, the grey plots have silt applied. c. Close-up of one pair of plots depicting depressions made by a nail and silt application to only one plot per pair. 135

Figure 4.2. Map of Alberta, Canada showing the location of Jasper National Park (gray shaded area) with an enlargement of Devona Flats region, the study area. Sites 1 – 3 along the Snake Indian River were used for log mapping and characterization. Log environmental measurements and gametophyte fragment regeneration experiments were located at sites A – C. 136

Figure 4.3. Comparison of log characteristics scored for 258 logs at sites 1 – 3 for logs without (unshaded) and with (shaded) *D. johansenii*: a. Maximum log height from the ground, b. Species richness, c. Maximum log diameter, d. Percent slope of logs, e. Decay stage distribution, and e. Silt layer presence/absence. For the box plots, the heavy horizontal bar represents the median. The box represents the range of 50% of the data while the vertical bars show the interquartile range. Circles and asterisks signify data outliers and extreme values. The number of logs included in each category is given below the x-axis. 142

Figure 4.4. Summary of mean environmental parameters measured at sites A – C on seven suitable (white) and unsuitable (black) logs per site. Error bars represent standard error of the mean. Parameters are the means from three replicates on each log (for seven logs, N = 21). a. Cumulative photosynthetically active light received from 20 May – 16 September 1999. b. Percent water lost from saturated sponges over five hours in August 1999. c. Mean biological temperature from 20 May – 16 September 1999. 145

Figure 4.5. Comparison of *Didymodon johansenii* gametophyte fragment survivorship at sites A, B and C on seven suitable (s) and seven unsuitable (u) logs per site, on no silt (white) and silt (black) plots. Error bars represent a standard error above and below the mean. Site and suitability are abbreviated on the x-axis below the number of logs. 147

Figure 4.6. Summary of *Didymodon johansenii* gametophyte fragment sprouting at sites A, B and C on seven suitable (s) and seven unsuitable (u) logs per site, on no silt (white) and silt (black) plots. Error bars represent a standard error above and below the mean. Site and suitability are abbreviated on the x-axis below the number of logs. 150

Figure 5.1. Map of study area showing general location of sites used for the six study species. Some sites are obscured because of close proximity to one another. There are five sites for all six species. Site symbols correspond to species symbols used throughout the figures in this paper: *M. macrocarpa* (●), *B. pseudotriquetrum* (○), *D. johansenii* (■), *D. rigidulus* var. *gracilis* (□), *M. arizonicum* (▲), and *M. spinulosum* (△). Inset map shows the province of Alberta and the position of Jasper National Park (gray) and the area of enlargement (rectangle) within Alberta. The cities of Edmonton (star) and Hinton (dot) are shown for reference. 165

Figure 5.2. Diagram depicting the relationship of fluorometer variables used in this study. F_o is the minimal or basal level of fluorescence emitted when a dark-adapted sample receives light from the modulating beam that is at an intensity too low to activate photosystem II. F_m is the upper or maximal fluorescence emitted by the plant when struck by a saturating flash of light that is bright but too brief to activate photosystem II. The difference between F_m and F_o is called variable fluorescence or F_v. F_v/F_m is the maximum quantum yield of photosystem II. A similar relationship exists for fluorescence measurements taken on light-adapted plants. Fluorescence reaches a steady state if the light intensity remains steady (F_t). In a light-adapted plant, effective maximal fluorescence (F_m') is lower than F_m because some of the light is being absorbed for photochemistry or dissipated as heat (non-photochemical quenching). The difference between F_m' and F_t over F_m' is the effective quantum yield of photosystem II (ϕPSII). Non-photochemical quenching (qN) = $(F_m-F_m')/F_m'$. Black arrows indicate activation of the measuring light and gray arrows indicate activation of a saturating flash. 168

Figure 5.3. Mean values for variables comparing the habitat environment of six moss species. a) Total mean net water gain (g) of sponges placed beside moss colonies at five replicate sites per species. Sponges were weighed every ten days throughout the 1998 growing season. b) Total mean water loss (% initial wet weight) from sponges (five per site) over 5 hours during sunny days with mean temperatures above 15°C in late August 1999 at three replicate sites per species. c) Cumulative light levels measured with photo sensitive diazo blueprint paper at five replicate sites per species. Higher number of exposed sheets corresponds to higher cumulative light intensities. Means with different letters are significantly different at $\alpha = 0.05$ using Tukey HSD post-hoc test. Symbols denote the mean and error bars are standard error. 177

Figure 5.4. Responses of fluorescence variables ϕPSII and qN to light flashes of increasing intensities for six moss species: a) Interpolation of values for each species showing the response of ϕPSII (% of original yield) to increasing light intensities. b) Interpolation of values for each species showing response of non-photochemical quenching (qN) to increasing light intensities. Quenching potential is saturated at a value of 1.0. 179

Figure 5.5. Yield (ϕPSII) recovery after 3 days of desiccation at 15°C, 20 μmol m^{-2} sec^{-1} and 80% relative humidity expressed as fitted curves for yield recovery over time. Yield recovery curves were fit with equations of the form, yield = (A*time)/(B+time), where yield is effective quantum yield of photosystem II, A is the asymptote, time is time after re-wetting in minutes, and B is the value of x when y = A/2. The control, non-desiccated sample, yield at 48 hours (2880 minutes) is presented for comparison. Species are abbreviated by the first letter of their genus and first three letters of their specific epithet. Rare species are in bold typeface and species symbols are the same as in previous figures. Symbols denote the mean and error bars are standard error. 182

Figure 5.6. Effect of storage condition and length of storage on fragment viability for six moss species, a-f. The rare species are in bold typeface. Mean number of viable fragments (± standard error) for six replicates with 20 fragments each. Differences in viability between wet and dry storage for each storage time were compared by one-way ANOVA and significance levels were adjusted for multiple comparisons. These differences are shown by time above the x-axis. The significance levels are: ns $p > 0.008$, not significant, * $p < 0.008$, ** $p < 0.0017$, *** $p < 0.00017$. The same controls were used for wet and dry treatments. 186

Figure 6.1. Summary of 4-month establishment plots for fragments recovered (a) and regenerating (b). *Mielichhoferia macrocarpa* (**Mmac**), *B. pseudotriquetrum* (Bpse), *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi) on the left were grown at native and non-native sites in 1998. Significance symbols above the species abbreviations denote planned comparisons on transformed data for native versus non-native fragment performance. Native site symbols are in black (rare) and white (common) and non-native sites are in gray. On the right, *D. johansenii* (**Djoh**), *D. rigidulus* (Drig), and the two species of *Mnium* establishment in 2000 is shown. Letters associated with native site symbols separate species into post-hoc groupings from Tukey post-hoc test ($p<0.0125$) for the four species comparisons in each year. Symbols denote the mean and error bars are standard error. 225

Figure 6.2. Summary of 16-month establishment plots for fragments recovered (a) and regenerating (b). *Didymodon johansenii* (**Djoh**), *D. rigidulus* (Drig), *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi) were grown at native and non-native sites from May 1999 - August 2000. Significance symbols above the species abbreviations denote planned comparison for native versus non-native fragment performance. Native site symbols are in black (rare) and white (common) and non-native sites are in gray. Letters associated with native site symbols separate species into post-hoc groupings from Tukey post-hoc test ($p<0.0125$) for the four species comparisons in each year. Symbols denote the mean and error bars are standard error. 226

Figure 6.3. Comparison of establishment ability for two species of *Mnium*, *M. arizonicum* (**Mari**) and *M. spinulosum* (Mspi) at native and non-native sites when planted alone and with neighbors. The effects of treatment on establishment are separated by fragment recovery (a) and fragment regeneration (b). Symbols denote the mean and error bars are standard error. 230

Figure 6.4. Comparison of colony expansion over three years showing the cumulative percent of colonies that expanded in size (stripes), remained the same size (gray), decreased in size (black), and disappeared (white) for five species of moss. Similar colony data for *D. rigidulus* was only obtainable after one year due to complete loss of mapped colonies after three years. Letters denote significant post-hoc differences between proportion of colonies that expanded between species. 233

Figure 6.5. Mean separation for *in situ* yield measurements taken on six species. Means with different letters were significantly different by Tukey HSD ($\alpha = 0.05$). *M. macrocarpa* (**Mmac,●**), *B. pseudotriquetrum* (Bpse,○), *D. johansenii* (**Djoh,■**), *D. rigidulus* (Drig,□), *M. arizonicum* (**Mari,▲**), and *M. spinulosum* (Mspi,△). Symbols denote the mean and error bars are standard error. 234

Figure 6.6. Comparison of percentage of green stems in four-month reciprocal transplants of stem bundles into neighbors at native and non-native sites for *M. arizonicum* (**Mari**) and *M. spinulosum* (Mspi). Significance symbols are for planned comparisons of performance at native versus non-native sites: ns, $p > 0.05$, * $p < 0.05$. Symbols denote the mean and error bars are standard error. 237

Figure 6.7. Percent of colonies that had disappeared after three years for six mosses, *M. macrocarpa* (**Mmac**), *B. pseudotriquetrum* (Bpse), *D. johansenii* (**Djoh**), *D. rigidulus* **(Drig)**, *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi). Letters above the bars show percentages that differed between species for disappeared (regular font) and disturbed (bold font) colonies in Tukey-type post hoc comparison ($\alpha = 0.05$). 238

Figure 6.8. Between species differences scored for frequency of neighbor encounter(inset) and relative percent of encounter outcomes. In the inset, post-hoc differences in percentage of neighbor encounters are shown by letters above the bars. Species with different letters are different by Tukey-type test for proportions ($\alpha = 0.01$). The legend pertains to differences in encounter outcomes. Species are abbreviated by the first letter of their genus and first three letters of their specific epithet. The letters denote species with different percentage of losses (Tukey-type test for proportions, $\alpha = 0.01$). 239

Figure 7.1. Representation of differences between a. dendrogram reflecting species phylogeny and b. dendrogram reflecting species rarity with the rare species in bold. The most important difference is the first dichotomy, which differentiates the diplolepideous mosses from the haplolepideous mosses (a) or differentiates rare species from the common species (b). Note that the more general term dendrogram is used in this chapter, although the dendrogram based on phylogeny could more specifically be called a cladogram. 260

Figure 7.2. UPGMA dendrogram showing species similarity for nine ecological traits relating to local persistence: *in situ* yield (ΦPSII), colony expansion (3 yrs), neighbor contact, disappeared colonies (3 yrs), neighbor encounters lost, regeneration ability (4 mos), fragment disappearance (4 mos), local abundance, and sporophyte frequency. Numbers at the dendrogram nodes represent the order of group joining and are referred to in the text summary. Rare species are in bold. 263

Figure 7.3. Colony disappearance, neighbor encounter, establishment ability and substrate restriction. Tracing of ecological traits on a dendrogram representing hypothesized evolutionary relationships of the six study species. White branch traits are: low disappearance of colonies, high neighbor contact, lack of establishment limitation and no substrate restriction. Substrate specificity is thought to be a derived trait within the Bryales (Vitt 1984), and all three species lacking substrate specificity occur on soil or humus. Gray branches have higher colony disturbance, lower neighbor contact, and substrate restrictions that correspond with establishment limitations. 267

Figure 7.4. Local abundance and neighbor encounter outcome. Dendrogram representing relationships among six moss species showing characters restricted to members of the family Bryaceae in this study. Gray branches represent the traits of high local abundance and low loss of neighbor encounters. The polarity of these characters within the Bryales is not clear, but their co-occurrence along phylogenetic lines is of ecological interest. White branches represent character states of low to medium local abundance and high loss of neighbor encounters. 268

Figure 7.5. Short-term and long-term desiccation tolerance. The co-occurrence of ecological traits on a dendrogram representing the current phylogenetic hypothesis for six taxa in the Bryales. Gray branches correspond with possession of both short- and long-term desiccation tolerance (i.e, long-term propagule viability in air storage). *Mnium spinulosum* possessed short- but not long-term desiccation tolerance indicated by a striped branch. Desiccation tolerance is thought to be a derived trait within the Bryales (Vitt 1984). White branches denote lack of these two traits. Rare species are in bold and all three possess desiccation tolerance and specialization for asexual reproduction. 269

List of abbreviations and symbols for study species

Study species:	**Abbreviation:**	**Symbol:**
Mielichhoferia macrocarpa	**Mmac**	●
Bryum pseudotriquetrum	Bpse	○
Didymodon johansenii	**Djoh**	■
Didymodon rigidulus var. *gracilis*	Drig	□
Mnium arizonicum	**Mari**	▲
Mnium spinulosum	Mspi	△

Chapter 1: General Introduction to rarity theory- does it apply to plants and how fully has it been tested?

"Who can explain why one species ranges widely and is numerous, and why another allied species has a narrow range and is rare?" - Darwin 1859

The study of rare organisms forms an essential part of understanding differences in species' abundance and distributions, a central goal in ecology. This thesis consists of several studies exploring the comparative ecology of three rare and three common moss species. Perhaps the greatest challenge in understanding rarity is posed by the paradox of whether a given trait is a cause or consequence of a species' rarity (Fiedler 1986, Fiedler & Ahouse 1992, Gaston & Kunin 1997). That is, did the plant species evolve the traits associated with rarity after being rare or did the species always have these traits, which predisposed the species toward becoming rare? Answering this question requires a great deal of knowledge concerning a species' evolutionary history. In this thesis I do not attempt to answer the ultimate question of whether current species traits are the product or cause of current distributions. Instead my studies focus on rare species in ecological time, and so the question is not why are the species rare (*sensu* Fiedler 1986, Fiedler & Ahouse 1992), but rather what factors are limiting the species *now*? And further, do rare and common moss species tend to have different ecological limitations or different intensities of these limitations?

This introductory chapter attempts to summarize current plant rarity concepts and theory and to review empirical research on ecological limitations of rare plant species. The literature is divided into three sections of inquiry: 1) how are rare species defined, 2) which traits are associated with rarity, and 3) what theories exist to explain rarity? Theory explaining differences in the abundance and range size of species has come mostly from the zoological literature and primary research for rarity in plants has been concentrated almost entirely on flowering plants. I summarize the existing literature on patterns of rarity in bryophytes and outline differences between bryophytes and angiosperms that may pertain to the ability, or lack thereof, of current rarity theory to encompass bryophytes. Finally, I propose a framework of limiting factors for mosses that forms the basis of the hypotheses explored in subsequent chapters.

Rarity definitions and terminology.

Rarity and commonness in the most basic sense are qualitative descriptions of species' occurrence. All the definitions of rarity from Darwin (1859) and his contemporaries to Gaston (1997) include components of species' abundance and range size. For at least a century and a half, rare species have been defined as species with low abundance and/or small range sizes. This general idea has yielded four general categories of species, over a variety of spatial scales (Table 1.1). Phytogeographical terms apply over the global scale while metapopulational terms, elaborated by Söderström's (1989) CURS model, apply to the population level (Table 1.1, Figure 1.1). The metapopulational terms of the CURS model, Core, Urban, Rural and Satellite, are therefore specific to the local scale, and a species may vary between categories in different parts of its range (Herben 1994). A similar problem arises with the categories of Rabinowitz (1981) because there is no consistency in definitions of "low" abundance and "small" range size (Gaston 1997, Gitzendanner & Soltis 2000). In this section, I will discuss qualitative types of rarity and reasons that a quantitative definition of rarity elludes us.

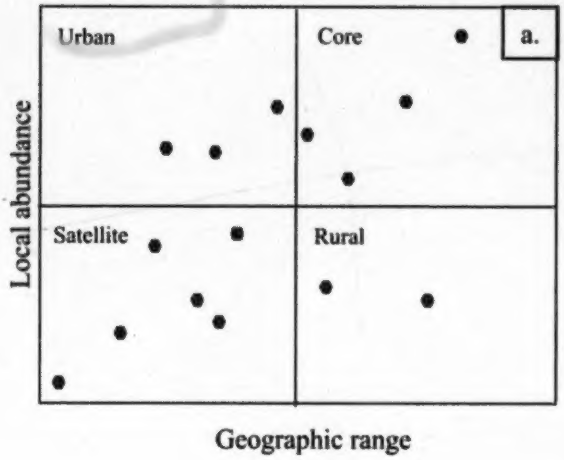
With consistency in the qualitative delineation of rarity over time, why have there been so many reviews of rarity concepts and definitions (e.g., Drury 1980, Stebbins 1980, Harper 1981, Fiedler 1986, Fiedler & Ahouse 1992, Gaston 1994, Kunin & Gaston 1997)? Part of the trouble in defining rarity comes from the negative definition of a rare species as being any species that is not common. In general, only the first category (Table 1.1), widespread over the area being considered and locally abundant, is considered as common. We have therefore lent all the clarity to common species and none to rare species. In reality neither rare nor common are monolithic. Rabinowitz (1981) eloquently demonstrated the diversitry of rare species, but perhaps the common species have been even more consistently viewed as one category. In 1981, Rabinowitz

Table 1.1. The four most general species distribution patterns and their relationship to terminology that has been used to describe them at varying spatial scales. The numbers correspond to categories depicted in Figure 1.1.

Scale: (source) **Distribution**	Global (Phytogeography*)	Global/Regional (Gleason 1924)	Regional: (Rabinowitz 1981)	Population level: (Hanski 1982; Söderström 1989a**)
1. widespread in area, locally abundant	Cosmopolitan	Common	Common	Core
2. restricted in area, locally abundant	Endemic to area	Rare	Restricted (rare)	Urban
3. widespread in area, locally rare	Disjunct	Rare	Sparse (rare)	Rural
4. restricted in area, locally rare	Endemic to area	Rare	Endemic (rare)	Satellite

*At the global scale, phytogeography naturally places more emphasis on overall distribution patterns and the terms imply little about local abundance.

**Hanski (1982) developed the terms core and satellite, while Söderström (1989a) contributed the terms urban and rural in his CURS model based on bryophyte distribution patterns.



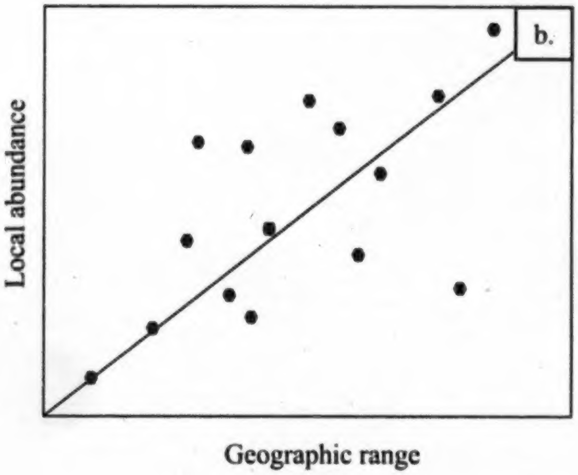


Figure 1.1. Two possible hypotheses on the relationship between species range size and local abundance: **a**. four distinct categories of the CURS model suggested by Söderström (1989), refer to Table 1.1, and **b**.continuous, positive linear relationship supported by Gaston (1996).

published the most widely cited and often used classification of rare plants in which she added the parameter of habitat specificity to Darwin's (1859) two categories of abundance and distribution to create a topology containing seven types of rare plants. Birks *et al.* (1998) examined moss and liverwort species of the British flora in relation to Rabinowitz's (1981) classification and concluded that "most bryophyte species are not common and many have a narrow habitat specificity." This habitat specificity is a function of bryophytes' smaller sizes and their ability to differentiate by colonizing different substrate types such as rock surfaces that are inhospitable to most root bearing plants.

Classification of bryophytes into Rabinowitz's (1981) categories pinpoints a key problem in quantifying rarity, that is, rarity is relative not absolute. If the same quantitative variables, e.g. range size and local abundance are used to classify all plant species, then species considered rare from one taxon may overlap with species considered common in another taxon in absolute terms of geographic range and local abundance. This overlap might be due to differences in the diversity of species within higher taxa, their evolutionary history and/or their age. Therefore, attempts at more quantitative inter-taxa definitions of rarity are confounded by the possibility that different taxa require different absolute values denoting "low" abundance and "small" range size.

Fiedler and Ahouse (1992) argued that Rabinowitz's (1981) classification fails to distinguish between species' attributes that may be either a result or consequence of rarity depending on species' history, such as habitat specificity and population size. They suggested a classification recognizing four categories of rare vascular plants based on species' temporal persistence and geographic distribution. This classification emphasizes the inevitable contingency of rarity definitions on spatial and time scales (after Gleason 1924).

Bevill and Louda (1999) questioned the utility of Fiedler and Ahouse's (1992) classification due to the lack of data on species' ages. However, if species' age is an essential part of defining rarity, then perhaps we should make an attempt to broadly define a species' age in terms of young versus old within a lineage. As Gleason (1924) noted from the age and area debate, although a rare species may be any age and both range contractions and expansions are likely throughout the history of a species, species' age remains inextricably linked to its range and abundance. One implication of age could be that young rare species are more likely to have always been rare than old rare species. A more serious problem with the Fiedler and Ahouse (1992) classification in relation to bryophytes is that almost all bryophytes fall into the one category, long temporal persistence and wide geographic range. The limited applicability of the classification to bryophytes relates to differences in lineage age and perhaps dispersability, with many bryophytes belonging to older lineages with perhaps greater dispersal ability than other embryophytes. Although considering bryophytes in relation to this rarity classification places them in relation to other embryophytes, it falls short of separating the bryophytes from one another in terms of rarity.

Another important distinction made when defining types of rare species is that between evolutionary and anthropogenic rarities (Fiedler 1986, Gaston & Kunin 1997). Evolutionary rarities are those species that are "naturally" rare within our historic time scale and anthropogenic rarities are those that historically were more widespread, but are known to have become rare due to human influence. This distinction implies that some rare species cannot be successfully conserved because their rarity resulted from factors beyond our manipulation, such as relictual species with limited genetic variability and species who have lost habitat from historical climate changes (Rosenzweig & Lomolino 1997). Some species are simply bound for extinction, although it still may be appropriate to consider whether or not our actions are bringing them to an untimely end. Kunin & Gaston (1997) also observed the possibility that "naturally" rare species may be evolutionarily adapted to their rare status means that "anthropogenic" rarities may need more immediate and intense management. In particular, Meagher *et al.* (1978) suggested that species with long life spans and low reproductive rates were in greater danger of extinction from human habitat alteration.

In summary, a qualitative definition of rarity is widely agreed to include components of geographical range and local abundance. These components create three natural distribution patterns for rare species. Species' age and human influence on species' rarity may be two additional components to consider when creating groupings of rare species that reflect common causes of rarity. The main problems associated with quantitative definitions of rarity are posed by the heterogeneous distributions and origins of rare taxa. Quantitative definitions for the four basic distribution types (Table1.1) may be possible; however, quantitative rarity definitions will always differ between higher taxa.

Patterns in rarity.

One of the most general and earliest patterns described for rare species was that rarity is common and commonness is rare (Raunakier's law of frequency, Gleason 1929, Preston 1948), that is, there are few species that are both widespread and locally abundant. Many of the earlier authors proposed explanations for rare species that made broad conclusions on the nature of rare plants (Table 1.2). Fiedler (1986) offered a thorough review of the historical rarity literature where many patterns were first proposed. I include these early theories here as ideas advanced for rare species rather than in the section on rarity theories because their observational nature does not offer testable hypotheses relevant to a range of rare species. In the words of Gleason (1924), "they succeed where they succeed and they fail where they fail."

One of the most well explored rare-common differences is whether rare species have less genetic variation than common species (Gitzendanner & Soltis 2000). In their review, Gitzendanner and Soltis (2000) conclude that while some rare species have lower genetic variation than their common congeners, it is an overgeneralization to say that all rare species have lower genetic variation. Rare species that have large local populations may have genetic variability equal to common congeners (Gitzendanner & Soltis 2000). We should also recognize that theories explaining why some rare species have low genetic variation do not necessarily explain why those species are rare.

Perhaps the greatest challenge in exploring traits associated with rarity is posed by the paradox of whether a given trait is a cause or consequence of a species' rarity (Fiedler 1986, Fiedler & Ahouse 1992, Gaston & Kunin 1997). That is, did the plant species evolve the traits associated with rarity after being rare or did the species always have these traits, which predisposed the species toward becoming rare? Answering this

Table 1.2. Early ideas concerning plant rarity and conclusions for rare plant limitations summarized from the review of Fiedler (1986).

Authors	Theory Rare species are rare because:	Implications/ mechanisms Rare species are:
Willis (1916, 1922); Wynne-Edwards (1937)	not enough time to disperse and increase their range	young species, dispersal limited
Darwin (1859), Fernald (1918, 1929, 1942, 1943)	old and senescent	old species, poor competitors
Cain (1940), Stebbins (1942)	lack ability to colonize new habitats	genetically homogenous, poor competitors
Griggs (1940)	can only inhabit places undesirable to other species	poor competitors
Wright (1956), Huxley (1963)	fixation of mutations or accumulation of mutations due to small population size	genetically homogeneous, genetically less fit
Lewis (1953a, 1953b, 1959, 1961, 1962) Lewis & Raven 1958 Raven (1964)	specialization, genotypic differentiation in response to extreme edaphic conditions	edaphically restricted, genetically more homogeneous

question requires a great deal of knowledge concerning a species' evolutionary history. Fiedler and Ahouse (1992) suggested that species of different age and geographic distribution have different ultimate causes of rarity. In addition to the four categories of rare species discussed earlier, Fiedler and Ahouse (1992) suggested that species of different age and geographic distribution have different ultimate causes of rarity. They proposed a hierarchy of nine factors that related to the ultimate cause of a species' rarity (Table 1.3; Fiedler 1986, Fiedler & Ahouse 1992). Fiedler and Ahouse (1992) ranked possible causes of rarity in order of their relevance for each of their four species categories, i.e, old taxon with wide range, young taxon with wide range, young taxon with narrow range and old taxon with narrow range. They noted that a taxon's ecology is the most likely cause of rarity for young species with narrow ranges (i.e., neo-endemic). Ecology was listed as secondary importance for the other three categories; however, for the old species the primary factors of earth and evolutionary history can hardly be of help in understanding proximal causes of rarity. As a result, one might also consider ecology as the most important proximal cause of rarity for these two classes of rare species.

Rosenzweig and Lomolino (1997) listed seven ecological traits of species that may predispose or cause their rarity (Table 1.3). Their list is remeniscent of some of the theories outlined in Table 1.2 in that it includes all the special cases that may cause rarity. Four of their species traits relate to habitat specialization, two to evolutionary history and one to competitive ability; some of these traits may not apply to bryophytes. In particular, the position of a species in a guild with distinct preferences may be irrelevant to bryophytes since there is evidence that bryophytes may all belong to the same guild (Bastow Wilson *et al.* 1995). There is limited data from Europe demonstrating that a bryophyte species has declined as a result of competition with an exotic species (Bates pers. comm., Stieperaere *et al.* 1997). In terms of testable hypotheses, species intolerance will be the most straightforward to investigate and as Rosenzweig and Lomolino (1997) suggest intolerance and the patterns that it produces may lend support for Brown's (1984, 1995) resource breadth or niche-based hypothesis discussed in the next section.

Table 1.3. Summary of recent approaches employed to discover patterns in rarity. The approach names as given by the authors are in bold. Fiedler and Ahouse (1992) suggest traits of species that need to be considered when exploring the causes of rarity. Rosenweig and Lomolino (1997) outline traits that pre-dispose species to becoming rare. Gaston and Kunin (1997) synthesize traits associated with rare species without implying whether they are a cause or consequence of rarity.

Hierarchies of cause (Fiedler & Ahouse 1992)	**Rare species candidate traits** (Rosenzweig & Lomolino 1997)	**Overall rare species traits** (Gaston & Kunin 1997)
- taxon age - genetics - evolutionary history - taxonomic position - ecology - population biology - reproductive biology - land use history - sensitivity to humans	- narrow fundamental niche, often with high competition - extreme niche within a guild, body size, larger species tend to be rare (animal based) - habitat dependent and habitat becomes rare through climate change - taxa with inherently narrow niches - product of centrifugal speciation - vulnerable to new competitive/exploitative interactions - populations are controlled by chaotic interactive dynamics (animal based)	- self-compatible or reproduce asexually - less investment in sexual reproduction - poor dispersers - use less common &/or narrower range of resources

Recently there have been many synthetic analyses to find traits that are more prevalent among rare species than common species or traits that relate to the geographical range of species. Several studies have compared floral morphology (Harper 1979, Hamilton 1990, Kunin & Shimida 1997), dispersal ability (Aizen & Patterson 1990, Oakwood *et al.* 1993, Thompson & Hodgson 1996) and overall morphological variability within species (Primack 1980, Rapson & Maze 1994 and references cited therein). Gaston & Kunin (1997) suggest several generalizations for differences between rare and common species from their synthesis of both animal and plant literature (Table 1.3). In general, they suggest that rare species are more likely to be self-compatible or reproduce asexually, to invest less in sexual reproduction, to be poorer dispersers, to use less common resources and/or a narrower range of resources. These limitations can be broadly divided into reproductive and resource limitations.

Some of these patterns have support in the bryophyte literature. In terms of reproduction, Longton (1992a) found evidence that certain reproductive systems are over represented in rare British mosses when compared to the whole British flora. In particular, there was a higher proportion (55%) of the rare species did not produce sporophytes compared to the total British flora (19%). A similar pattern has been found for British hepatics (Laaka-Lindberg *et al.* 2000). This pattern suggests that rare moss species may be reproductively limited either by lack of mates, self-incompatibility or environmental constraints. In dioicous (i.e., unisexual gametophyte) species, sporophyte production requires both male and female individuals present within a short distance for the sperm to travel from the antheridia to the archegonia. In monoicous (i.e, bisexual gametophyte) species, self-incompatibility may explain a lack of sporophyte production, although this has not been documented (During & van Tooren 1988). Hedderson (1992) considered moss rarity at range limits and found that mosses are more likely to switch from sporophyte production to asexual reproduction at the edges of their range. These studies suggest dioicous mosses and mosses at their range limits are dispersal limited by low sporophyte production.

In terms of resource limitations, Shaw (1981) observed that *Pohlia* species with more narrowly restricted habitat requirements (e.g. *Pohlia camptotrachela* and *P. filum*) are also more geographically restricted and exhibit less morphological variability than more widespread common species (e.g. *Pohlia annotina* and *P. drummondii*, respectively). There is evidence both for and against this trend in vascular plants (Primack 1980, Rapson & Maze 1994).

Vitt and Belland (1997) described the attributes most prevalent among rare mosses of Alberta, Canada. They found that several characters including acrocarpous growth form, stress tolerator life strategy, and alpine habitat were over represented in the rare species flora when compared to the occurrence of these characteristics in the non-rare moss flora. The prevalence of alpine habitat for rare Alberta mosses may relate to habitat restrictions of these mosses; however, this restricted distribution pattern does not clarify whether the species are limited by abiotic or biotic factors.

Rarity in theory

Hutchinson's (1957) niche theory offers a logical starting point for testing limitations on species' abundance and distributions. The niche was defined as a multidimensional space bounded by abiotic and/or biotic limitations. The fundamental niche is bounded only by abiotic environmental limitations on the species. The differences between a species' realized and fundamental niche are the result of biotic interactions (Hutchinson 1957). Therefore, the study of a species' local niche should include some comparison of fundamental and realized niche to determine the relative importance of biotic and abiotic factors in defining the species' spatial distribution (e.g., Austin *et al.* 1990, Birks *et al.* 1998).

Stebbins (1980) offered the first theory intended specifically to explain plant rarity which he termed the gene pool – niche interaction theory. The theory suggests that rare species, specifically endemics, are the result of an interaction between localized environmental conditions, lack of genetic diversity which inhibits expansion into surrounding environments and the effects of past climate on population distributions. While Stebbins' theory was the first to flesh out the complexity of studying causes of rarity, it did not lend itself to the formulation of testable hypotheses (Fiedler 1986).

The fact that some species are more widespread and common than other species, i.e., have wider realized niches, begs the question of whether common species are simply more tolerant, i.e. also have wider fundamental niches. Brown (1984, 1995) shows evidence for this in vascular plants and birds and proposes a twofold theory that expands on this basic idea. Brown (1984) postulated 1) that a general relationship between species' abundance and range size exists based on the spatial autocorrelation of environmental variables such that species abundance is greatest in the center of its range and decreases at the periphery, and 2) that among similar species there is a positive correlation between local population density and range.

The largest group of hypotheses relevant to studies of rarity has developed in an attempt to explain the positive relationship between local abundance and range size. This relationship would suggest that the four categories of species' distributions in Table 1.1 could be replaced by a continuum (linear relationship) between local abundance and range size (Figure 1.1). Gaston in particular has championed this view (Gaston 1996, Gaston *et al.* 1997, Kunin & Gaston 1997, Thompson *et al.* 1998). In their comprehensive review, Gaston *et al.* (1997) described theories that have been proposed to explain the positive local abundance–range size relationship (Table 1.4). I interpreted these theories in terms of the predictions that they make for rare species (Table 1.4). The range position theory does not offer a hypothesis relevant to the ecological characteristics of rare versus common species, however, the other five theories do. These five theories suggest rare-common differences stem from differential: 1) habitat tolerances, 2) habitat use, 3) competitive abilities, 4) dispersal abilities and 5) reproductive and survival rates. These theories emphasize the importance of understanding the ecology of a species to explore why it is rare or common. In other words, despite the influence that evolutionary and earth history may have on abundance of a species, theories formulated to address the broad pattern of a positive relationship between the abundance and distribution of a species all focus on ecological explanations.

Table 1.4. Current biological hypotheses that have been proposed to explain positive interspecific abundance-range size relationships (based on Gaston *et al.* 1997) and their implications/ predictions for rare species relative to common species. Hypothesis numbers correspond to Tables 1.5 and 1.6. Range position is not considered further and so is not numbered here (see text for more detail).

Hypothesis name (origin)	**Prediction for rare species**
Range position (Grinnell 1922)	species become rare at their range limits
1. Resource breadth (Brown 1984)	rare species have smaller resource niche breadths than common species
2. Resource availability (Hanski *et al.* 1993)	rare species use resources that are rare
3. Habitat selection (O'Connor 1987)	rare species have smaller niche breadths as a result of inability to overcome intra- or inter- specific competitive effects
4. Metapopulation dynamics (Hanski 1991, includes CURS model)	rare & common species may have similar niche breadths, but rare species have poorer dispersal abilities & lower population growth rates
5. Vital rates (Holt *et al.* 1997)	rare species have lower maximum population growth rates due to lower reproduction &/or higher mortality

Autecological plant studies.

Several studies emphasize the importance of experiments to pinpoint why individual species are rare (Bevill & Louda 1999, Gaston & Kunin 1997, Lahti *et al.* 1991). Bevill and Louda (1999) reviewed vascular plant studies that compare attributes of rare and closely related common species, and found that measured species characteristics varied widely from study to study. Therefore, they could not perform a meta-analysis to test for commonalities in ecological characteristics of rare vascular plants. In addition to this criticism, 72.6 % of 149 studies reviewed here were on narrow endemic, flowering plants (Appendix A). Other types of rarity studied were anthropogenic rarities (11.6%), species at their range limits (10.9 %), sparse species (2.7%), and disjunct species (2.2%). *Solidago shortii* and *Pedicularis furbishiae* are the most well studied species with six and five studies, respectively (Appendix A).

Comparative studies on rare and common species in the same genus have been conducted for 13 genera, and 89% of the comparative studies are on narrow endemics. The rare species with two or more comparative studies are *Echinacea tenneseensis*, *Erythronium propullans*, *Solidago shortii* and the *Calochortus* lilies (Appendix A). No one limitation was most prevalent in these studies. Eight ecological limitations were found: poor dispersal (2 spp.), disturbance regime requirements (2 spp.), poor competitive ability (2 spp.), reproductive biology (low pollination) (6 spp.), habitat specificity (2 spp.), low establishment (1 spp.), preferential herbivory (1 spp.) and inability to adapt to historical climate change effects (4 spp.). Only comparative studies were able to conclude that historical limitations were important. It seems probable that this limitation may have applied to other species if they had been compared more closely with a common congener. When all the rare species studies aimed at discerning species limitations are considered together (149 total), no new categories of limiting factors were added to the list, although several aspects of reproductive biology other than pollination were found to be limiting, especially low seed set. Historical factors were supported in eight studies; however, we are concerned with proximal factors here. Reproductive biology and habitat specificity were the two limiting factors most often considered; however, of the proximal causes considered disturbance regime was most often limiting whenever it was considered (Table 1.5). The most important component of the habitat seemed to be not the habitat *per se*, but the disturbance regime, especially the fire regime (e.g., Boucher 1981, Deyrup & Menges 1997, Lesica 1999, Moll & Gubb 1981, Quintana-Ascendio & Morales-Hernandez 1997). There are currently no rarity hypotheses which explicitly incorporate disturbance regime requirements (Table 1.5), although some may consider this limitation to be grouped with habitat specificity. The most frequently considered limitation (53% of the studies) was reproductive biology, most often pollination limitations.

The most frequently found limitations in decreasing order were disturbance regime requirements, poor dispersal, poor competitive ability, habitat specificity, differential mortality, reproductive biology (especially, low pollination, low seed set) and low establishment (Table 1.5). Whether the limitations found in these studies are actually the most limiting factors for the species may vary with the number of factors and species considered in the studies. As the majority of studies were not comparative, it is difficult to decide whether the limitations found truly contribute to the species rarity. In addition, forty-four (30%) of the studies did not consider any limitations other than the ones that they found to be limiting and twenty-seven studies (17%) found no limitation for the species studied (Appendix A). Forty-four percent of the studies found only one limitation, 23% found two limitations, 6% found three limitations, and 3% had four limitations.

In conclusion, there were eight main limiting factors extracted from the existing literature of 149 studies (Appendix A, Table 1.5). Two of the factors, historical limitation and disturbance regime requirements, were found in almost all of the studies where they were considered. However, historical limitations are not proximate and are difficult to test experimentally and disturbance regime requirements are often considered as part of habitat specificity in theory. In addition, in 76% of the studies in which disturbance regime limitations were supported, another ecological factor was also limiting (Appendix A). Dispersal, competitive ability, habitat specificity, herbivory, reproductive biology, and establishment were all found in roughly half of the studies

Table 1.5. Literature review of autecological studies on rare vascular plant species. The table summarizes results for 130 species from 149 studies summarized in more detail in Appendix A. Relevant hypothesis refers to rarity hypotheses by their numbering in Table 1.4. Here the number of species considered for a limitation and the number that were limited by that factor are presented. There were eight main limiting factors found for vascular plants. The limitation numbers given here correpond to those used in Appendix A. For several categories there was a more specific limitation stated and the number of species with the specific limitation are given in parentheses beside the totals.

Limiting factor	Relevant hypothesis	Consider limitation	Limitation found	Found/consider (%)
1. Historical, climate change	1, 2	8	8	100
2. Disturbance regime (fire)	none?	31	29 (13)	93.5
3. Poor dispersal (seed bank)	4	23	15 (5)	65.2
4. Low establishment	5	42	20	47.6
5. Poor competitor	3	27	17	63
6. Differential mortality (herbivory)	5	31	18 (16)	58
7. Reproductive biology (pollination)	5	81	40 (20)	49.4
8. Habitat specificity	1, 2	57	34	59.6

where they were considered (Table 1.5), and therefore seem equally likely to limit rare species. No one limiting factor emerged as dominant.

Rarity in Bryophyta: comparison to vascular plants.

In contrast to the many studies that have been conducted for rare flowering plants (Appendix A), there have only been a handful of studies on the demography (Furness & Hall 1981, Hancock & Brassard 1974, Lloret 1991) or population genetics (Shaw 1993, Shaw & Schneider 1995, Shaw 2000) of rare mosses. The demographic studies have been observational and there is a need for research aimed at experimentally discerning rare moss species' limitations. This paucity of rare bryophyte literature is the result of undercollection of bryophytes in general and the concomitant lack of reliable documentation of rare bryophytes in many parts of the world. In North America, the quantification of rarity for bryophyte species only exists in a few well-collected areas (e.g., Slack 1992). Consequently, bryophyte species preservation has relied on conservation areas established for reasons other than the presence of rare bryophyte populations (Hedderson 1992). The urgency of rare population management mandates that have motivated much of the research on rare flowering species do not exist for bryophytes.

Therefore, rather than a literature review of empirical studies this section will be more broadly based. I use the eight limitations found in the previous section for rare flowering plants as a template for presenting what is known about each of these limitations for mosses in general. There are many differences between the demography and ecology of flowering plants and bryophytes and these will be outlined here with the aim of hypothesizing differences in the relative importance or application of angiosperm limitations to bryophytes.

Dispersal.—In general, moss species are more widespread than flowering plant species (Schofield 1992, Tan & Pócs 2000). If bryophyte and flowering plant floras are compared at the same scale, there are proportionally fewer endemic bryophyte species and genera (Tan & Pócs 2000). In terms of disjunctions, patterns observed at the generic level in vascular plants are similar to patterns observed at the species level in mosses

(Delgadillo 1995). Whether these differences in the overall distribution of mosses compared to seed plants reflect differences in the ages of these plant groups or their relative dispersability is still unclear (Schofield 1992). Differences in the overall distribution patterns of bryophytes may mean that some hypotheses such as resource breadth may be more applicable to mosses since they are a group with low endemism.

A strong relationship between dispersal ability and range size has been documented for tropical bryophytes (van Zanten & Pócs 1981, van Zanten and Gradstein 1988). There was a strong correlation between tolerance of spores to desiccation, freezing and UV exposure (conditions that would be experienced during long distance dispersal) and the range size of a species (van Zanten & Pócs 1981, van Zanten & Gradstein 1988). In particular, spores of endemic liverwort species had less dispersal ability than spores of wide ranging species. Recently, Thompson *et al.* (1999) emphasized that "by far the best evidence for a link between range and dispersal is found in mosses, where the dispersal mechanism (spores) is presumably highly effective and the distinction between well-dispersed species (regular sporophyte production) and poorly dispersed species (no sporophyte production) is particularly clear." Although this "link" seems well supported, it is not entirely clear what role spores play in moss establishment. Because of the relatively high importance of desiccation tolerant asexual vegetative diaspores in dispersal of bryophytes when compared to vascular plants, the dispersal of spores for mosses should not be equated (in terms of establishment importance) with seed dispersal. However, as in other land plants, the importance of spores in establishment of mosses seems to vary greatly depending on life strategy (Miles & Longton 1990, During 1997). Experimental sowing of spores in the field has resulted in no or very low establishment (Miles & Longton 1990, Keever 1957) for all but the weediest of species (e.g., *Funaria hygrometrica*) and the larger role of asexual reproduction in bryophyte ecology has gained wide acceptance (Newton & Mishler 1994, Slack 1997). Several authors (Watson 1981, Li & Vitt 1994, 1995, Longton 1994, Mishler & Newton 1988) have suggested that chemical inhibition may explain the lack of spore germination in the field.

Reproductive biology.—Bryophytes obviously do not have pollen or pollinator limitations; however, they may have other reproductive limitations. In terms of sexual reproductive limitations, dioicous mosses could face limitations related to the distance between male and female plants, while monoicous mosses may experience problems based on the increased likelihood of self-fertilization. The evidence for the limitation of sexual reproduction in monoicous mosses is much weaker than for dioicous mosses (Longton 1994). There are many dioicous species that are not known to produce sporophytes anywhere and often these species occur in highly disjunct populations containing only female or male plants (Longton & Schuster 1983, Longton 1992a). The increased difficulty of sexual reproduction in dioicous mosses may explain why specialized asexual propagules are more frequent in dioicous mosses (Imura 1994, Longton 1992a), although this pattern does not hold for liverworts (Laaka-Lindberg *et al.* 2000).

American populations of the rare moss, *Scopelophila cataractae,* where sporophyte production is unknown and all populations are either male or female present an interesting case in point (Shaw 1993). Shaw (1993) suggested that the most likely explanation for this pattern was long distance dispersal of asexual diaspores (in this case, plant fragments) for two reasons. First, the species does not produce sporophytes in North America but moss fragments of the species can remain dormant for several years, and second, the species occurs on substrates, such as mine tailings, that have only been available for colonization in recent history (Shaw 1993). Despite the likely asexual origin of the *S. cataractae* populations, they were shown to possess a great deal of morphological and physiological variability when grown on different soil types.

In general, there has been very little research on moss reproductive limitations (During & van Tooren 1987, Longton 1994). Moss sperm usually only travel a few centimeters in terrestrial situations although splash cups may increase this distance to a meter (Longton & Schuster 1983, Wyatt & Anderson 1984) and invertebrate transport may play a role in lipid containing sperm masses (Paolillo 1981). For bryophytes in general, the paucity of specialized gamete transfer mechanisms together with the prevalence of asexual reproduction makes a primary reproductive limitation less likely than in flowering plants. Consequently, I argue that the patterns documented by Longton (1992a) between sporophyte production and species' rarity are probably more an effect rather than a cause of rarity at least for dioicous mosses. Likewise, the pattern of decreased sexual reproduction by mosses at their range limits (Hedderson 1992) might reflect the effect of adverse environmental conditions that result both in species' rarity and lack of sporophyte production.

Disturbance regime.—The prevalence of asexual reproduction in mosses relates not only to the difficulty of fertilization, but also perhaps to the prevalence of disturbance in the life cycle of plants that lack stabilizing roots. As a result, mosses possess more means of continuous dispersal throughout a given year. Although mosses differ from each other in regards to life span, spore size and sporophyte frequency (i.e., life strategies of During 1992), within the plant kingdom most mosses may be viewed as stress tolerators or ruderals (Grime *et al.* 1990). In general, bryophytes appear as if they are engineered to avoid environmental fluctuations while angiosperms are engineered to withstand them (Proctor 2000).

Although rhizoids may help in stabilization, bryophyte species lack roots to secure them to their substrate and are often influenced by small-scale disturbances such as those produced by small rodents. For instance, the importance of small-scale disturbances to the establishment of mosses on logs has been demonstrated by Kimmerer and Young (1996). The diaspore bank, analagous to the seedbank, has been documented in grassland and forest systems (During & ter Horst 1983, During 1997, Jonsson 1993), and it may allow species with long-lived diaspores that are able to survive *in situ* to respond faster to these small-scale disturbances than species without long-lived propagules. Bryophyte diaspores not only include spores but also a vast array of asexual propagules such as plant fragments, gemmae, rhizoidal fragments, protonemal fragments, bubils, and specialized fragile leaf tips. Mosses respond to disturbance much more frequently and at a much smaller scale than vascular plants and it may be that humans have less overall impact on disturbance regimes affecting mosses or that mosses respond to many kinds of disturbance in the same way. Since disturbance is common in the life cycles of most bryophytes, a disturbance limitation resulting in a short-lived suitable habitat will likely be concurrent with a dispersal limitation in rare mosses. Söderström's

(1987, 1989) work with epixylic mosses has demonstrated this point, as well as, the applicability of metapopulation theory to these bryophytes.

Fire regime was an important limiting factor for many rare vascular plants in that many of those species studies require the disturbance caused by fire to arest succession and create sites for establishment (Table 1.5, Appendix A). In contrast, very little is known about the role of fire in moss ecology. The first species to recolonize after a fire are generalist pioneer species (e.g., *Funaria hygrometrica*, *Ceratodon purpureus*, *Bryum argenteum* and *Polytrichum piliferum*) that colonize after many types of disturbance (Esposito *et al.* 1999, Puche & Gimeno 2000, Thomas *et al.* 1994).

Establishment ability.—Perhaps formation of a protonemal mat from a spore is most ecologically analogous to the seedling stage, but the protonema may also originate from vegetative propagules and in at least some mosses protonema are more ecologically flexible than seedlings. Protonema of several species have been shown to be desiccation tolerant and produce asexual diaspores such that both the protonematal strands and their gemmae serve as additional means of asexual dispersal (Duckett *et al.* 1998).

Establishment appears to play a very important role in the composition of bryophyte communities (Kimmerer & Young 1996, Li & Vitt 1994, 1995). Establishment restrictions strongly influence the patterns of species substrate and microtopographic specificity that we perceive in mature communities. Current literature suggests that establishment ability may be more important limitation for rare bryophyte species than for rare vascular plants. Mosses seem to be particularly sensitive to substrate chemistry during establishment (e.g., Thomas *et al.* 1994) and there is also evidence that biotic chemical inhibition may also be important in determining establishment success (Watson 1981, Newton & Mishler 1994).

Competition.—Earlier observers of bryophyte communities hypothesized a minimal role for competition in structuring bryophyte communities (Slack 1990). This view can be traced to the overall ruderal and stress tolerator strategies of bryophytes and the inherent dominance of disturbance in controlling species' distributions. However, individual moss species do have different capacities for taking advantages of temporally available resources implying that some species are better competitors than others (Grime *et al.* 1990), and competition between bryophytes has been documented in more stable habitats such as grasslands and peatlands (Rydin 1997, Zamfir & Goldberg 2000). The lack of evidence for competitive effects among adult bryophytes has led several researchers to hypothesize that for mosses competitive interactions may be most influential during the establishment stage (Watson 1981, Rydin 1986, Li & Vitt 1995, Rydin 1997, Slack 1997). Marino (1991) found differences in the abilities of four entomophilous moss species to establish in species mixes from spores on wet versus dry dung. Similarly, through experiments using bryophyte fragments, Zamfir and Goldberg (2000) reported the existence of a competitive hierarchy for seven grassland moss species. Despite some evidence of competitive effects during establishment, competitive exclusion has not been documented in mosses.

Competition during the establishment stage can take many forms including differential diaspore production, diaspore longevity, and diaspore sensitivity to the presence of other species (and perhaps their chemical exudates). For instance, in a bryophyte colonization experiment the number of diaspores produced by a species per unit time was concluded to be the most important factor explaining which species became dominant in permanent plots (van Tooren & During 1988). The role of competitive ability in distinguishing rare and common moss species has never been explored, although it seems likely that such a difference should be tested in the establishment stage.

Habitat specificity.—In general, mosses are more habitat specific than vascular plants and many authors have hypothesized that the availability of suitable habitats is the main factor explaining bryophyte species rarity (Vitt & Belland 1997, Tan & Pocs 2000). Resource limitations have been investigated for bryophytes (e.g. niche theory reviews Slack 1990, 1997); however, there has been no direct comparison between the resource use or breadth of rare and common species. Data from a few existing studies may help to evaluate the resource breadth hypothesis for bryophytes. Shaw (1981) and Horton (1988) suggested that rare moss species tend to have narrower edaphic requirements than more common species. For propaguliferous *Pohlia* species, Shaw (1981) notes a correlation between "ecological amplitude" (which seems comparable to niche breadth), geographic distribution and the degree of morphological variability. By re-analysis of the data presented in Horton (1988), common *Encalypta* species (per Horton (1983)) were found to have significantly wider average niche breadths for pH and organic matter content than species cited as rare (Mann Whitney U, p= 0.006 and 0.035, respectively). Existing evidence suggests that habitat limitations may be very important in explaining the difference between rare and common moss species.

Historical climate change.—Given the relatively greater importance of habitat specificity of bryophytes than vascular plants in conjunction with the older ages of most bryophyte clades, it seems likely that habitat loss due to climate change may be an important ultimate cause of rarity in bryophytes. Many widely disjunct species are thought to have survived overall climate change *in situ* by persisting in microhabitats that still reflect those past climate conditions (Crum 1972). In the context of this study, however, this ultimate limitation would have to be correlated with a proximal habitat specificity requirement.

Herbivory.—Generally, bryophytes are not viewed as having many natural enemies and evidence for herbivory on bryophytes when compared to lichens or vascular plants appears inconsequential (Longton 1992b). Gerson (1982) suggested herbivory is limited by bryophyte chemical defenses. The actual mechanisms accounting for infrequent herbivory on bryophytes are still unclear. The sporophytes may be more liable to predation, especially by ants (Gerson 1982), and such predation could lower dispersal ability of a species.

Evaluation of current rarity theory.

In my previous review of autecological studies on rare vascular plants, I discovered that the importance of the disturbance regime was the one major limitation that is not really addressed by any of the existing rarity hypotheses (Table 1.4). However, several studies did explore limitations encompassed by the existing rarity theory. In this section, I attempt to put results and conclusions from comparative plant studies into the perspective of current rarity theory. I have selected both empirical and synthetic studies that specifically discuss the predictions made by theory for rare species (Table 1.4) in order to answer the following set of questions: Do results from empirical and synthetic comparative studies support or lack support for current rarity hypotheses? Is any hypothesis particularly well supported or wholely untested? Do bryophyte and vascular plant studies vary in which hypotheses they support?

Studies that examined rare species trends in a flora mainly support the resource availability hypothesis, while empirical comparative studies largely support the vital rates hypothesis (Table 1.6). This disagreement may reflect the fact that some of the hypotheses lend themselves to testing through synthetic approaches while others can only be tested empirically because the detailed information that they require (e.g., population growth rates) are not available at the scale of floras. The metapopulation dynamics theory has not been adequately addressed in the plant literature (Table 1.6). This may be because it makes fairly complex set of predictions for rare species requiring tests of niche breadth, dispersal and population growth rates.

Studies from the bryophyte literature support the resource breadth hypothesis, while support for this hypothesis is lacking in the vascular plant studies (Table 1.6). This probably reflects a greater habitat specificity of bryophytes and may also reflect lower endemism in rare bryophytes. Burgman (1989) found no support for the resource availability hypothesis in his analysis using a flora where the rare species were almost all endemic to the study region. It may be that the rarity of neo-endemics, which appear more prone to dispersal limitations, may be better described by metapopulation dynamics than resource breadth. There are no data available in the bryophyte literature with which to test the four hypotheses other than resource breadth (Table 1.6).

Thesis framework.

Throughout this chapter I have emphasized both the importance of ecological studies to understanding rarity and the importance of studies within the Bryophyta to test and perhaps broaden the current theorhetical framework for understanding rarity in general and plant rarity in particular. Prior ecological studies of rare bryophytes have been scarce and limited to mosses with very specialized life strategies (Furness & Hall 1981; Hancock & Brassard 1974; Lloret 1991). There are currently no comparative ecological studies of rare bryophytes that include a variety of rare species and life

Table 1.6. Studies on rare species whose data and/or stated conclusions pertain to recent theories explaining rarity. Theory predictions for rare species are outlined in Table 1.4. Studies from the bryophyte literature are in italics. Both synthetic and empirical papers are included here. Synthetic studies are in bold. Metapopulation dynamics theory requires documentation of both dispersal limitation and lower population growth rates (Table 1.4) and none of the reviewed studies include both of these measurements.

Theory name (source)	studies in support	studies that lack support
1. Resource breadth (Brown 1984)	*Horton 1988*, *Shaw 1981*	Baskin *et al.* 1997, **Burgman 1989,** Prober 1992, Rabinowitz *et al.* 1986, 1989
2. Resource availability (Hanski *et al.* 1993)	**Hodgson 1986, Lahti *et al.* 1991, Thompson *et al.* 1998, Thompson *et al.* 1999, *Vitt & Belland 1998***	
3. Habitat selection (O'Connor 1987)	Baskin *et al.* 1997, Prober 1992	
4. Metapopulation dynamics (Hanski 1991)		
5. Vital rates (Holt *et al.* 1997)	Byers & Meagher 1997, Fiedler *et al.* 1998, Morley 1982, Rabinowitz *et al.* 1989	Baskin *et al.* 1997*, Stanley *et al.* 1998*

* Both of these studies found historical limitations, so they do not really support any of the ecologically based theories here.

strategies. There are also no studies comparing the ecology of rare species to closely related common species, a method that has been employed in several vascular plant studies (Appendix A).

If one removes pollination and herbivory (which do not apply to bryophytes) from the list of limitations found for flowering plants, then the resulting list should form a rational basis for exploring moss species limitations. However, these potentially limiting factors can be viewed as either hierarchical or interactive (Figure 1.2). Hierarchical arrangement of limiting factors assumes that only one factor can limit a species (Figure 1.2a). In contrast, an interactive limitation model allows for limitation by more than one factor or by the interaction of factors (Figure 1.2b). Do mosses tend to be limited primarily by one factor or several interacting factors? The answer to this question is far from clear in the bryophyte literature. Several studies have found one factor such as dispersal (Söderström 1987; Söderström 1989b; Söderström & Jonsson 1989) or habitat (Heegaard & Hangelbroek 1999) to be most limiting the distribution of a species. Other studies suggest that moss limitations are the sum and interaction of several factors such as disturbance, dispersal and establishment (Kimmerer 1994; Kimmerer & Young 1996) or habitat, establishment and competition (Marino 1991).

The hierarchical view of limitations can be argued based on the order in which the factors take place in the life cycle (Figure 1.2a). Dispersal and microhabitat availability are the first factors that may limit the distribution of a moss. If the moss cannot disperse to the available substrates either because of its insufficient dispersal capabilities or because of the rarity of its required substrate, then it will be a rare moss. Establishment abilities of the moss will come into play once the moss has successfully dispersed to available suitable substrates. If the moss diaspores are very short lived or have a very low germination/regeneration rate, then regardless of dispersal distance or substrate availability, the moss will still be rare.

Although attractive in the simplicity that it implies, the hierarchical view has several limitations. In a hierarchical scenario, competition is unlikely to be a primary limitation since it will only be so if none of the preceeding factors were limiting. In addition, disturbance, which may affect many stages of the life cycle, is impossible to

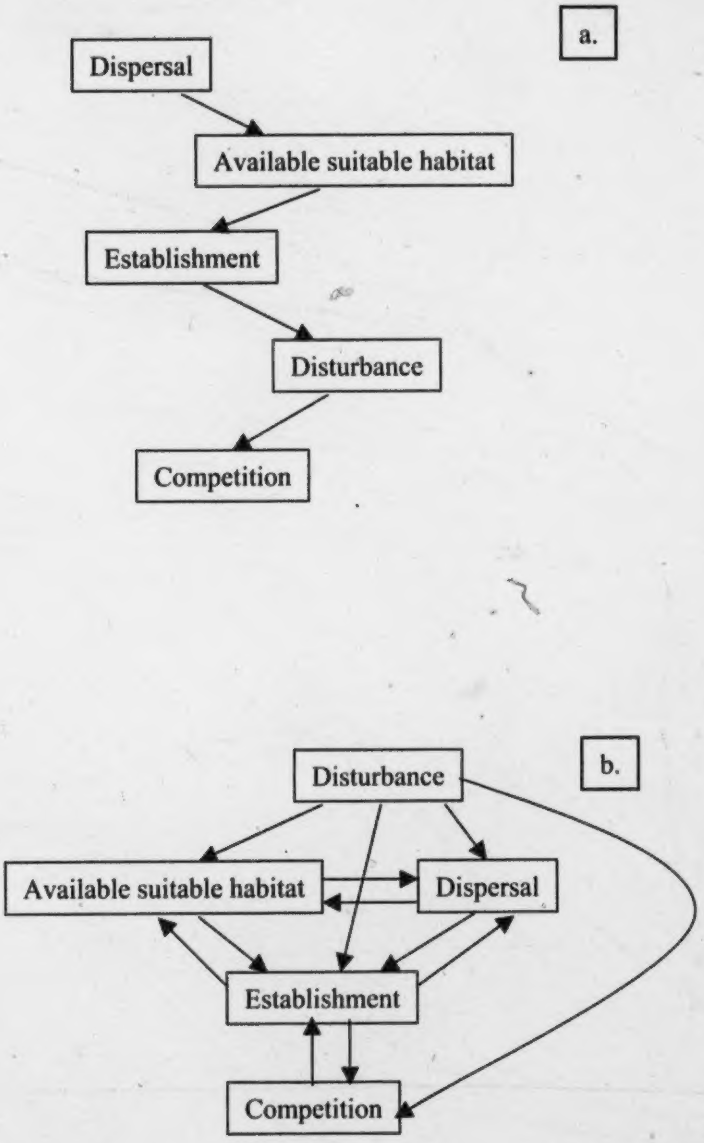

a.
Dispersal
Available suitable habitat
Establishment
Disturbance
Competition
b.
Disturbance
Available suitable habitat
Dispersal
Establishment
Competition

Figure 1.2. Conceptual models of how limiting factors might interact to influence species distribution: **a.** hierarchical and **b.** interactive.

order in the hierarchical view. In other words, studies that assume one factor is primarily limiting are destined to conclude that this factor is either dispersal or habitat. Because of these limitations, the hypotheses posed in this thesis will be based on an interactive view of limiting factors (Figure 1.2).

Conclusion.

The search for consistent rare-common differences has escalated in the past decade perhaps partially in response to increasing political awareness of the vulnerability of rare species and hence the need for rare species' management strategies (Gaston 1994, Kunin & Gaston 1997, Bevill & Louda 1999). Most of the hypotheses currently proposed to explain the positive relationship between local abundance and range size have not been tested for plants. The literature available for decisions in rare plant management consists almost exclusively of studies on endemic flowering plants. Bryophytes offer a unique plant lineage on which to test and perhaps develop our knowledge base.

I propose that there are ecological differences between rare and common moss species on a local scale that relate to the differences in their global abundance. Further, these differences may not be the same for all rare/common pairs, but will be expressed either as differences in the limiting factors themselves or in the intensity of the limitations that these factors impose. I will look for differences in limitations in terms of resource (habitat) breadth, substrate tolerance, dispersal potential, establishment ability, and competition and disturbance pressure.

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Chapter 2: Study species synopsis- selection criteria, background and relative rarity.

Clear species selection criteria and background information on the study species are crucial in a thesis based on autecological experimentation because hypotheses and methods are often species specific. I begin with a discussion of study species selection, taxonomic relationships within the rare-common species pairs, and general species morphology. Three species pairs were chosen for this study using the following criteria: 1. The species concepts are widely accepted and clearly delimited. 2. Rare species are considered rare at many scales, in Alberta, North America and globally. Actual listing of the species as rare was only available for Alberta, where the species were categorized as either S1, five or fewer occurrences or S2, 5-20 occurrences in 1996. 3. Common species have a close taxonomic (and where information is available, phylogenetic) relationship and similar ecology to the rare species and are documented as widespread in Alberta and North America. Choosing species with similar evolutionary history and present day habitat use controls for species traits that could be misinterpreted as being associated with rarity when those traits are in fact the result of shared evolutionary history or life strategy (Fiedler 1987, Harvey & Pagel 1991). Of the 279 moss species listed as rare (S1-S3) in Alberta (ANHIC 2001), 188 have common congeners in the Province, and 180 of these common congeners are widespread in North America. The three pairs were chosen mainly for logistic reasons such as their potential for accurate field identification and our knowledge of exact site locations. The three species pairs, with the rare species listed first, are: 1. *Mielichhoferia macrocarpa* (Hook.) Jaeg. and *Bryum pseudotriquetrum* (Hedw.) Gaertn. *et al.*, 2. *Didymodon johansenii* (Williams) Crum and *Didymodon rigidulus* Hedw. var. *gracilis* (Hook. & Grev.) Zander, and 3. *Mnium arizonicum* Amann and *Mnium spinulosum* Bruch. & Schimp. In tables and figures throughout this thesis the rare species will be in bold typeface. Abbreviations used for the species are the first letter of the genus and first three letters of the specific epithet (Table 2.1).

Table 2.1. Species names, abbreviations and general morphological comparison of plant size and colony habit. Values are compiled from Crum and Anderson (1981) and Lawton (1971) for *B. pseudotriquetrum* and *M. spinulosum*, Lawton (1971) for *M. macrocarpa*, *D. johansenii* and *M. arizonicum*, and Zander (1981) for *D. rigidulus* var. *gracilis*. Rare species are bolded.

Species name	Abbreviation	Leaf length (mm)	Plant height (cm)	Colony habit
Mielichhoferia macrocarpa	**Mmac**	0.6-1.5	0.3-1.0	dense cushions
Bryum pseudotriquetrum	Bpse	2.5-4.0	1.5-11	loose cushions, turves
Didymodon johansenii	**Djoh**	0.5-1.6	0.3-0.4	dense cushions
Didymodon rigidulus var. *gracilis*	Drig	0.8-3.0	1.0-2.0	turves
Mnium arizonicum	**Mari**	2.5-4.0	1.0-2.0	cushions, turves
Mnium spinulosum	Mspi	2.5-5.0	0.5-2.5	cushions, turves

Mielichhoferia macrocarpa and *Bryum pseudotriquetrum.—Mielichhoferia macrocarpa* and *B. pseudotriquetrum* are currently classified in separate genera; however, DNA sequencing data and phylogenetic analyses have shown *M. macrocarpa* belongs in the genus *Bryum* (Cox *et al* 2000). The relationship of *M. macrocarpa* to *B. pseudotriquetrum* remains unclear, although it seems most likely that they belong to different sections within the genus *Bryum*. *Mielichhoferia macrocarpa* resolves in a clade with members of section Bryum while *B. pseudotriquetrum* most likely belongs in section Cerniubryum (C. Cox pers. comm.). *Mielichhoferia macrocarpa* plants are relatively small and grow in short, compact cushions. *Bryum pseudotriquetrum* typically has stems 2-5 times longer than *M. macrocarpa* and forms less densely packed cushions or turves (Figure 2.1a, Table 2.1). Definitions for cushions and turves follow During (1992) as growth forms and Bates (1998) as life forms.

Didymodon johansenii and *D. rigidulus* var. *gracilis.*—Based on morphological evidence, both the *Didymodon* species are classified in the same section, Didymodon, within their genus (Zander 1998). There are no molecular data on relatedness available for these species. *Didymodon johansenii*, the smallest study species, grows in short, densely packed cushions (Figure 2.1b, Table 2.1). *Didymodon rigidulus* var. *gracilis* is generally taller than *D. johansenii*, although plants are often buried by soil for most of their actual height. Perhaps partly as a result of shifting soil, *D. rigidulus* var. *gracilis* plants form turves rather than cushions (Figure 2.1b, Table 2.1).

Mnium arizonicum and *M. spinulosum.— Mnium arizonicum* and *M. spinulosum* are both in the section Spinosa based on morphological characters (Koponen 1968). As with the *Didymodon* species, there are no molecular data pertaining to the phylogenetic relationship of these two moss species. The *Mnium* species are most equivalent in plant size and habit and both grow in loose cushions and turves (Figure 2.1c, Table 2.1).

Summary.—Given our current concepts of study species relationships, species within pairs are in the same genus and, additionally, *Didymodon* and *Mnium* species pairs are within the same section of their respective genera. Of the three species pairs, morphologically, the *Mnium* species are the best match (Figure 2.1). *Mielichhoferia macrocarpa* and *B. pseudotriquetrum* differ from one another the most in terms of plant

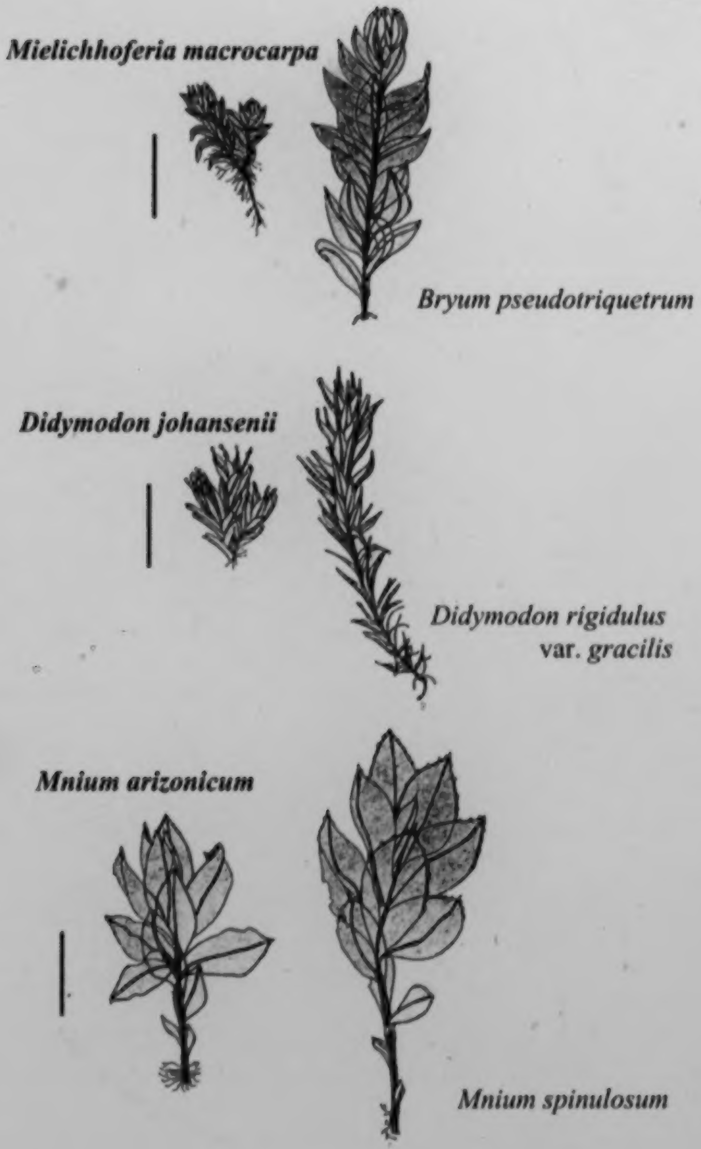

Mielichhoferia macrocarpa
Bryum pseudotriquetrum
Didymodon johansenii
Didymodon rigidulus var. *gracilis*
Mnium arizonicum
Mnium spinulosum

Figure 2.1. Habit sketches of one plant for each study species showing morphological differences. The scale bar is 0.4 cm for all three pairs. The rare species are on the left with their names bolded.

size, while *D. johansenii* and *D. rigidulus* var. *gracilis* differ most in colony habit (Table 2.1). The tendency for the rare species to be smaller here is notable because this pattern has also been found by Hedge and Ellstrand (1999) in the Californian and British vascular floras.

Geographic distributions of species pairs.

Distribution information is presented here for the species within Alberta, North America and globally. Personal observations on species distributions within Alberta are compiled from examination of herbarium specimens in the University of Alberta herbarium (ALTA) and personal field notes. Geographic distributions are defined here to include both species frequency and range area.

Mielichhoferia macrocarpa and *B. pseudotriquetrum.— Mielichhoferia macrocarpa* is known from seven localities in Alberta and twenty localities in North America (Table 2.2, Brassard & Hedderson 1983). The species is also reported from three localities outside of North America, southern Siberia, the southern Ural Mountains and the Sayan Mountains of central Asia (Ignatov & Afonina 1992, Shaw & Rooks 1994).

Bryum pseudotriquetrum is common throughout Alberta and North America (Crum & Anderson 1981, Lawton 1971). It is among the most widespread moss species on the planet with a worldwide distribution of: "Greenland to Alaska and south to California, Arizona, Colorado, Arkansas, and Florida; northern and southernmost South America; throughout Europe and across Asia to Japan; reported from Australia, New Zealand, Antarctica, Kerguelen, Réunion, several parts of Africa, and the Azores" (Crum & Anderson 1981). It is absent from tropical and subtropical lowlands (Ochi 1994).

Didymodon johansenii and *D. rigidulus* var. *gracilis.—Didymodon johansenii* is known from nine localities (seven of which are in Jasper National Park) in the montane *Picea glauca* floodplains of Alberta (pers. obs.). *Didymodon johansenii* is usually described as a rare circum-arctic species (Crum 1965, Zander 1998) and has been particularly well documented in arctic Alaska (Steere 1978). There are about twenty-five sites known for *D. johansenii* in North America (Table 2.2). The species occurs in

Table 2.2. Reference table of study species occurrence in Alberta and North America and globally. Rare species are in bold typeface immediately before their species partner. Ranks are assigned relative only to the other study species and are meant to illustrate rather than quantify differences between species. Ranks are relative to the study species and were assigned with 1 = smallest distribution. For sum of ranks, the lowest possible score is 2 and the highest is 11.5.

Species	Alberta:		North America:		Global:		Sum of Ranks
	# of sites	Extent	# of sites (rank)	Extent	Continents (rank)	Distribution	
Mmac	7	Rocky Mts only	20 (1)	AB, AK, NF, MT, CO, UT, Greenland	2 (2)	Holarctic, disjunct, montane	3
Bpse	100+	throughout	1000+ (5.5)	throughout	7 (6)	Cosmopolitan	11.5
Djoh	9	Rocky Mts only	25 (2)	AB, AK, NWT	3 (3)	Holarctic, disjunct, Arctic-montane	5
Drig	25+	prairie & montane	100+ (4)	throughout	4 (5)	Northern hemisphere	9
Mari	25+	Rocky Mts only	30+ (3)	AB, AZ, BC, CO, NV, UT, WY, NWT, Greenland, Mexico	1 (1)	North American endemic, western mountains & Arctic	4
Mspi	100+	boreal forest & Mts	1000+ (5.5)	boreal zone, mixed spruce forest	3 (4)	Circumboreal	9.5

several locations south of the Arctic especially in mountainous areas including the Canadian Rocky Mountains (Crum 1965), the Austrian and Swiss Alps (Kucera 2000), the Slovakian Belaer Mountains (Pilous 1995), and mountain ranges in Chinese Inner Mongolia and Tibet (Tan & Yu 1997). In Alberta, *D. rigidulus* var. *gracilis* occurs at lower elevations throughout the prairie and it is frequent in the montane ecoregion of Jasper National Park (pers. obs.). *D. rigidulus* var. *gracilis* occurs in North and Central America, Europe, the Middle East and Asia (Zander 1981, 1994).

Mnium arizonicum and *M. spinulosum.— Mnium arizonicum* is reported from twenty-five localities in Alberta (Table 2.2), and its occurrence has been observed as widespread and predictable in the Alberta Rockies (pers. obs., Lawton 1971). It can grow in close proximity to *M. spinulosum* at elevations as low as 1400 m (pers. obs., J. Doubt pers. comm.). *Mnium arizonicum* is known mainly from alpine and subalpine sites in the Rocky Mountains; however, it has also been reported north in the Canadian Arctic and Greenland (Koponen 1972) and south in Baja California (Koponen 1994). The species is considered to be a North American endemic, although Koponen (1972) speculates that it may eventually be found elsewhere in the Arctic.

The common species, *M. spinulosum* occurs in mesic *Picea glauca* and *Picea-Abies* stands throughout mountainous and boreal Alberta (pers. obs., Lawton 1971). It is found throughout the Boreal Zone in North America, Europe and Asia (Koponen 1981). *Mnium spinulosum* also extends somewhat south of the Boreal forest in eastern North America (Maryland; Crum & Anderson 1981) and western Europe (Iberian Peninsula, Spain; Fuertes & Acón 1999).

Summary.—The overall score for each species, based on number of known occurrences in Alberta, North America and globally, arranges the species from smallest to largest distribution as: *M. macrocarpa*, *D. johansenii*, *M. arizonicum*, *D. rigidulus* var. *gracilis*, *M. spinulosum* and *B. pseudotriquetrum* (Table 2.2). *Didymodon johansenii* and *M. arizonicum* have similar rank sums, but for different reasons. Both *D. johansenii* and *M. macrocarpa* are rare disjuncts, while *M. arizonicum* is considered rare because it is endemic to western North America. Disjunct and endemic species often have different causes of rarity (Fiedler & Ahouse 1992). *Didymodon rigidulus* var. *gracilis* has a larger overall range than the circumboreal *M. spinulosum*, but is not as frequent as *M. spinulosum* within its broader range. *Bryum pseudotriquetrum* has the broadest range and is frequent throughout the majority of its distribution.

Research study sites.

The remainder of this chapter presents species background information gained primarily from original data gathered in the field and growth chambers. Study site details are presented for all of the field sites used in the thesis (Table 2.3, Figs. 2.2-4). In general, a site is an area that contains the species of interest. Individual sites may be quite close (Figure 2.3-4); however, there is always a clear discontinuity in species occurrence (i.e., a clear boundary) between two sites. Boundary examples include roads, exposed ridge tops, and bare rock face. An effort was also made to choose sites with different aspects.

All study sites are located in the eastern Front Ranges of the Canadian Rocky Mountains, in Jasper National Park and Whitehorse Creek Wildland Park, Alberta, Canada (Fig. 2.2). There are 38 sites in total detailed in Table 2.3. Sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum* are located largely within the Whitehorse Creek Wildland Park (1600-2000m) (Fig. 2.3). *Mnium spinulosum* sites are located at lower elevation sites, 1400m, and *D. johansenii* and *D. rigidulus* var. *gracilis* sites are located at the lowest elevations (1050-1150m) in the montane ecoregion of Jasper National Park (Fig. 2.4). Mean daily temperatures and precipitation for January and July are given for four reporting stations in the study area (Table 2.4). Robb station is closest to Whitehorse Creek Wildland Park and the *M. spinulosum* sites. Two of the *M. arizonicum* sites are located at Grave Flats and this is the highest elevation reporting station in the area (Table 2.4). The *Didymodon* sites are generally warmer and drier than the sites outside of Jasper National Park (Table 2.4). Mean daily precipitation from June to August (the main growing season) is 298.3mm in Robb, 288.4mm at Grave Flats and 156.7mm in Jasper (Environment Canada 1998).

Studies conducted at each site are summarized in Table 2.3 along with notations on the chapters where these studies are presented. For local abundance estimates, colony

Table 2.3. Reference table of study sites summarizing map reference number for Figures 2.3-4, site location, elevation, and studies conducted at the site. The abbreviations used for studies conducted at each site followed by the chapters where the studies are presented are as follows: M = colony assessments by mapping (2,6), C = neighbor contact assessment (2,6), H = habitat quantification: pH, % OM, temperature & light (2,3,4,5), W = moisture quantification (2,3,4,5), EA = establishment and adult transplant experiments (6), F = *in situ* chlorophyll-fluorescence comparisons (6), SE = silt experiment (4).

Map #	Figure #	Site name	Location description	Latitude (N)	Longitude (W)	Elevation (m)	Studies conducted
1	2.3	**Mmac 1**	Mountain Park, 1st creek north	52°56.7	117°18.2	1790	M/C, H, W, EA, F
2	2.3	**Mmac 2**	Whitehorse Creek, across from campground	52°59.1	117°20.5	1600	M/C, H, EA, F
3	2.3	**Mmac 3**	Whitehorse Creek, 3 km upstream	52°59.2	117°22.5	1605	M/C, H, W, EA, F
4	2.3	**Mmac 4**	Whitehorse Creek, 3 km upstream	52°59.2	117°22.5	1605	H, EA
5	2.3	**Mmac 5**	Whitehorse Creek, last tributary, 1km upstream	52°58.9	117°21.3	1700	H, EA
6	2.3	**Mmac 6**	Drummond Creek	52°58.7	117°22.8	1690	H, W, EA
7	2.3	**Bpse 1**	Mountain Park, 1st creek north	52°56.7	117°18.2	1790	M, H, W, EA, F
8	2.3	**Bpse 2**	Cardinal Divide, 1st creek south	52°53.5	117°13.0	1810	M, H, EA
9	2.3	**Bpse 3**	Mountain Park, 2nd creek north	52°56.8	117°18.0	1780	H, EA, W

Table 2.3. Continued.

Map #	Figure #	Site name	Location description	Latitude (N)	Longitude (W)	Elevation (m)	Studies conducted
8	2.3	Bpse 2	Cardinal Divide, 1st creek south	52°53.5	117°13.0	1810	M, H, EA
9	2.3	Bpse 3	Mountain Park, 2nd creek north	52°56.8	117°18.0	1780	H, EA, W
10	2.3	Bpse 4	Whitehorse Creek, 1km upstream	52°59.2	117°21.5	1605	H, EA, F
11	2.3	Bpse 5	Whitehorse Creek, last tributary, 1km upstream	52°59.0	117°21.3	1690	M, H, EA, W
12	2.3	Bpse 6	Mountain Park, 2 km downstream (north) on McLeod River	52°56.8	117°17.7	1755	C, F
13	2.4	Djoh 1	Snake Indian River, north bank	53°09.1	118°00.8	1005	M, H, EA
14	2.4	Djoh 2	Snake Indian River, south bank	53°09.0	118°00.7	1005	M, H, EA
15	2.4	Djoh 3	Snake Indian River, south bank, farthest upstream	53°09.1	118°01.0	1020	H, EA
16	2.4	Djoh 4	Snake Indian River, north bank, farthest downstream	53°09.3	118°00.5	1005	H, EA
17	2.4	Djoh 5	Devona warden cabin	53°08.8	118°00.6	1020	M, H, EA

Table 2.3. Continued.

Map #	Figure #	Site name	Location description	Latitude (N)	Longitude (W)	Elevation (m)	Studies conducted
18	2.4	**Djoh A**	Devona Flats Dyke, Snake Indian River	53°09.5	117°59.8	1000	SE, W
19	2.4	**Djoh B**	Athabasca & Snake Indian River confluence	53°11.1	117°59.2	995	SE, W
20	2.4	**Djoh C**	Rocky River	53°08.6	117°58.5	1005	SE, W
21	2.4	**Djoh D**	Jasper Lake north end pull-off from Hwy 16	53°08.0	117°59.0	1005	F
22	2.4	**Djoh E**	between Devona CN station and Jasper Lake	53°08.6	117°59.8	1005	C
23	2.4	**Drig 1**	Snake Indian River, north bank slope above Djoh 1	53°09.2	118°00.7	1040	H, EA, W
24	2.4	**Drig 2**	Snake Indian River north bank slope, farthest upstream	53°09.3	118°01.1	1040	M, H, EA, W
25	2.4	**Drig 3**	Snake Indian River, north bank slope, ridge top	53°09.3	118°00.8	1090	M, H, EA, W
26	2.4	**Drig 4**	Snake Indian River, south bank slope	53°08.9	118°00.7	1050	H, EA
27	2.4	**Drig 5**	Snake Indian R., s. bank slope	53°08.9	118°00.7	1050	M, H, EA

Table 2.3. Continued.

Map #	Figure #	Site name	Location description	Latitude (N)	Longitude (W)	Elevation (m)	Studies conducted
28	2.4	Drig 6	Talbot Lake Hill, south end	53°04.8	118°01.5	1050	C, F
29	2.3	Mari 1	Cardinal Divide, east ridge	52°54.3	117°14.4	2015	M, H, EA, W, C, F
30	2.3	Mari 2	Grave Flats Tower, west slope	52°53.4	116°59.6	2030	H, EA, F
31	2.3	Mari 3	Cardinal Divide, west ridge, south facing	52°53.4	117°14.8	2000	H, EA, W
32	2.3	Mari 4	Cardinal Divide, west ridge, north facing	52°53.6	117°15.3	2005	M, H, EA, W
33	2.3	Mari 5	Grave Flats Tower, south slope	52°53.3	116°59.4	2025	M, H, EA
34	2.4	Mspi 1	east side of Cold Creek Road, 3 km from NW intersection w/Hwy 40	53°18.5	117°35.0	1400	M, H, EA
35	2.4	Mspi 2	east side of Cold Creek Road, 4.5 km from NW intersection w/Hwy 40	53°18.2	117°34.6	1400	H, EA
36	2.4	Mspi 3	west side of Cold Creek Road, 4.5 km from NW intersection w/Hwy 40	53°18.1	117°34.6	1400	M, H, EA

Table 2.3. Continued.

Map #	Figure #	Site name	Location description	Latitude (N)	Longitude (W)	Elevation (m)	Studies conducted
37	2.4	Mspi 4	west side of Cold Creek Road, 2 km from SE intersection w/Hwy 40	53°16.9	117°32.7	1400	H, EA, C
38	2.4	Mspi 5	east side of Cold Creek Road, 5 km from SE intersection w/Hwy 40	53°17.7	117°33.8	1400	M, H, EA

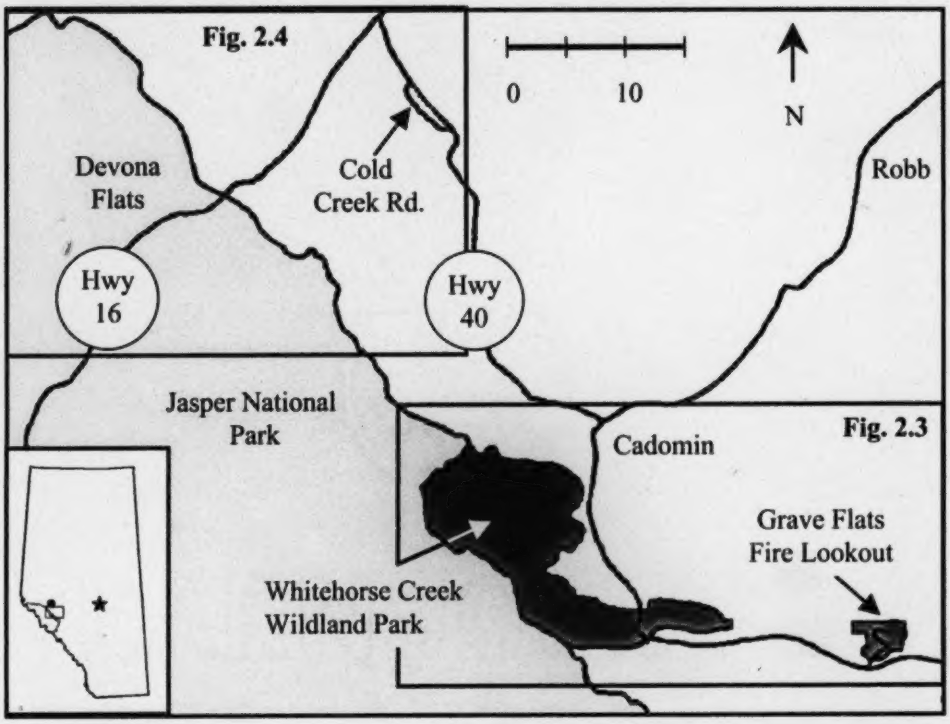


Fig. 2.4
0
10
N
Devona Flats
Cold Creek Rd.
Robb
Hwy 16
Hwy 40
Jasper National Park
Cadomin
Fig. 2.3
Grave Flats Fire Lookout
Whitehorse Creek Wildland Park

Figure 2.2. Map of study region showing location of study area in Alberta, Canada (inset) and two main areas of study in the front ranges of the Rocky Mountains. On the inset map of Alberta, the star is Edmonton and the dot is Hinton. The study area enlarged here is the rectangle and Jaspernational Park is the shaded region. The area containing Cadomin is enlarged in Figure 2.3 and includes sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum*. The area encompassing Devona Flats is enlarged in Figure 2.4 and includes sites for *D. johansenii*, *D. rigidulus* var. *gracilis*, and *M. spinulosum*.

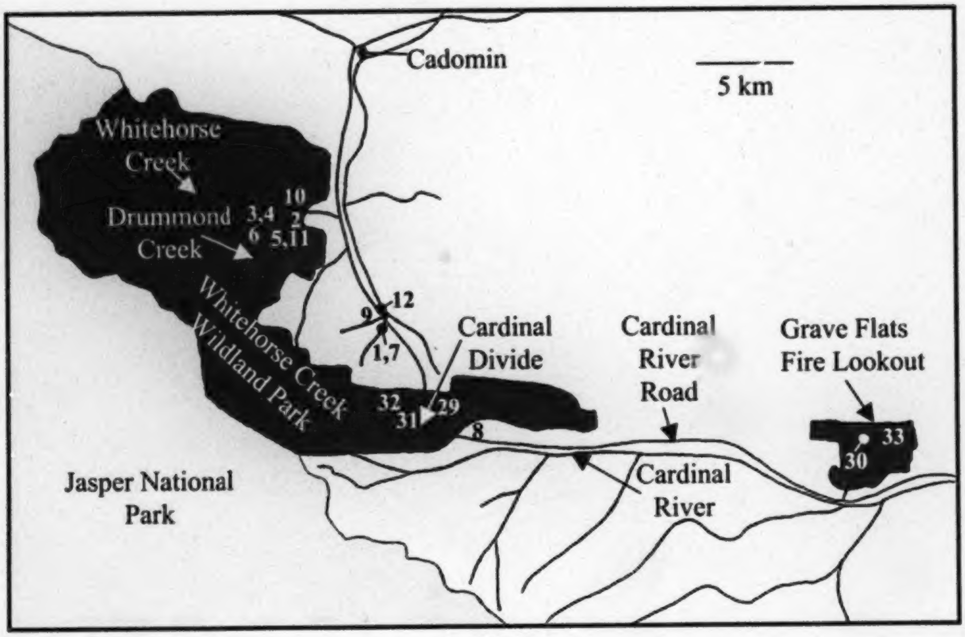

Cadomin
5 km
Whitehorse Creek
Drummond Creek
3,4
10
2
6
5,11
Whitehorse Creek Wildland Park
9
12
1,7
Cardinal Divide
Cardinal River Road
Grave Flats Fire Lookout
32
31
29
8
33
30
Jasper National Park
Cardinal River

Figure 2.3. Map of sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum*. Site numbers correspond to map #'s in Table 2.3. *Mielichhoferia* sites are numbers 1-6. *Bryum* sites are numbers 7-12, and *M. arizonicum* sites are numbers 29-33.

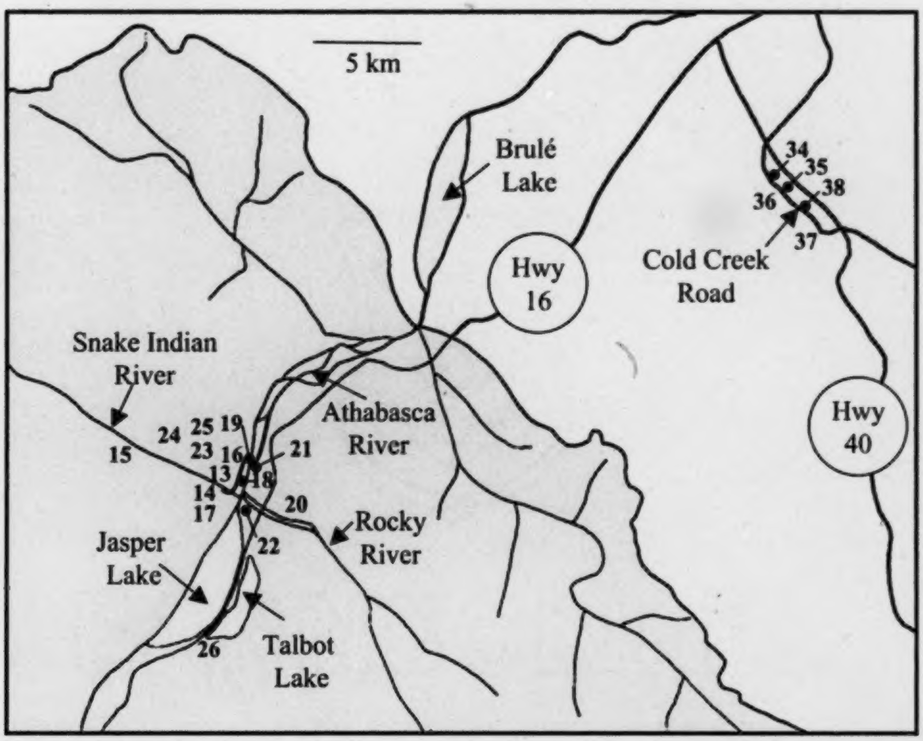

5 km
Brulé Lake
Hwy 16
Cold Creek Road
Hwy 40
Snake Indian River
Athabasca River
Rocky River
Jasper Lake
Talbot Lake
13
14
15
16
17
18
19
20
21
22
23
24
25
26
34
35
36
37
38

Figure 2.4. Map of sites for *D. johansenii*, *D. rigidulus* var. *gracilis*, and *M. spinulosum*. Site numbers correspond to map #'s in Table 2.3. *Didymodon johansenii* sites are numbers 13-22. *Didymodon rigidulus* var. *gracilis* sites are numbers 23-28. *Mnium spinulosum* sites are numbers 34-38. Light gray area marks Jasper National Park.

Table 2.4. Climate normals from four recording stations in the study area. Data are from the Canadian climate normals 1961-1990 (Environment Canada 1998).

Recording Station	Latitude (N)	Longitude (W)	Elevation (m)	Daily mean temperature (°C)		Daily mean precipitation (mm)	
				January	July	January	July
Robb	53°14'	116°14'	1130	-10.9	14.1	38.4	109.4
Grave Flats	52°51'	117°51'	2074	---	9.8	---	110.2
Jasper East	53°14'	117°14'	1003	-8.7	15.0	---	---
Jasper	52°53'	118°53'	1061	-10.7	15.1	31.1	56.2

mapping data were collected at three sites per species, neighbor contact assessments consisted of three random transects at one site per species (except for *M. macrocarpa*, see chapter 6 methods for details). Habitat measurements, establishment experiments and adult transplants were made at five sites for each species with establishment experiments and transplants also made at the five sites of the respective pair species.

Local abundance of study species.

Local abundance is a simple concept that is difficult to quantify using consistent criteria because species occur at different spatial scales and in varying dispersion patterns. Ideally, measurements of site area would be included; however, site boundaries often occur at too large a scale to delimit and measure accurately. Local abundance might also include a standard measure of site coverage or site frequency within a specified area on the landscape; however, detailed and complete documentation of moss species occurrence and site dimensions at the landscape scale is not available in Alberta and such data are beyond the scope of this research. Therefore, I equate the term local abundance with average percent cover of a species at a site. I use colony area and density to estimate average percent cover within a site. Data for quantifying local abundance was collected by mapping at least fifty colonies at three sites per species and by colony dimensions measured as part of competition transects. Colony mapping techniques varied between species because the species occur at different spatial scales (Table 2.5). Individual species mapping methods are described in Chapter 6 where the mapping data are used more fully to look at changes in colonies over time. Neighbor contact assessments were conducted at one site per species containing at least 150 colonies of the species that had not previously been used or affected by this study. At each site, three restricted random 1m wide belt transects were run with transect length varying along with the distance required to intersect fifty colonies per transect. Sampling sizes for colony data are smaller for *B. pseudotriquetrum* and *M. macrocarpa* because colony mapping methods for *B. pseudotriquetrum* did not involve colony area measurements and *M. macrocarpa* neighbor encounter and colony mapping data were obtained from the same set of colony tracings (Table 2.5, see Methods Chapter 6). Colony area estimates are

Table 2.5. Summary of study species' local abundance based on colony area, density and site area. Mean percent cover is calculated by mean colony area and density (i.e., mean area required to encounter 50 colonies). Rare species abbreviations are in bold. The overall rank is based on mean percent cover at a site where 1 = least abundant and 6 = most abundant.

Species	# of colonies	Colony area (cm^2)			Site area 50 colonies (m^2)		Mean % site cover	Rank
		Mean (stdev)	Median (range)	Rank	Mean (stdev)	Min-max		
Mmac	260	22 (27)	11 (172)	3	0.71 (0.31)	1 – 3	0.15	5
Bpse	150	690 (5100)	34 (59,350)	5.5	6.06 (2.83)	1 – 10^6	0.60	6
Djoh	303	10 (19)	4.2 (162)	2	56.42 (55.14)	5 – 250	0.0009	2
Drig	300	3 (7)	0.75 (352)	1	1.01 (0.85)	5 – 500	0.015	4
Mari	298	130 (160)	60.25 (1032)	5.5	1092 (265)	1 – 10^6	0.0006	1
Mspi	299	70 (110)	34.5 (1403)	4	180 (52)	10 – 10^8	0.002	3

based on length and width measurements. Comparison of within species-pair colony sizes were made on 150 colonies using Wilcoxon signed rank test.

Differences in site scale are summarized as range in study site areas. The mean area required for encountering fifty colonies of a species was used as a proxy for differences in species density. The area to include fifty colonies is used for between species comparisons because both the mapping and competition transect data were based on the first fifty colonies encountered. This area was calculated from mapping data by first calculating colony density for each species as: number of colonies mapped / mapped area. Colony density (colonies/m^2) was then converted to the area required to capture fifty colonies: 50 colonies / colony density. For *D. johansenii* and *M. arizonicum*, extra calculations were required because of the patchiness of their habitat at the site scale. For these two mosses the average number of colonies per habitat (i.e., habitat equals log for *D. johansenii* and tree clump for *M. arizonicum*) was calculated to derive the number of habitats required for fifty colonies. Within a site, number of logs or tree clumps with the moss species present were divided by the site area to obtain habitat density (i.e., logs/m^2 or clumps/m^2). The area to capture fifty colonies is then: # of habitats for 50 colonies / habitat density within site.

For a final expression of overall local abundance, I calculated percent cover of each species within a site from mean colony size and density: percent cover = [(mean colony size x 50) / mean site size for 50 colonies] x 100. Differences in species density and percent cover were not compared statistically because of the small sample size (N = 3 sites) per species.

M. macrocarpa and *B. pseudotriquetrum.—Bryum pseudotriquetrum* colonies are significantly larger ($p<0.001$) than *M. macrocarpa* colonies and less densely spaced (Table 2.5). *Mielichhoferia macrocarpa* sites are most often orders of magnitude smaller than *B. pseudotriquetrum* sites (Table 2.5, pers. obs.). Mainly due to smaller colony areas, *M. macrocarpa* colonies have lower average percent cover at a site than *B. pseudotriquetrum* (Table 2.5). Colony area and percent cover of *M. macrocarpa* are likely limited by disturbance from falling ice and rock (pers. obs.).

Didymodon johansenii and *D. rigidulus* var. *gracilis.*—*Didymodon rigidulus* var. *gracilis* colonies are on average a third the size of *D. johansenii* colonies and are significantly smaller ($p<0.001$); however, the maximum size of *D. rigidulus* var. *gracilis* colonies was three times the maximum size of *D. johansenii* colonies (Table 2.5). *Didymodon rigidulus* var. *gracilis* colonies are more densely situated within a site (Table 2.5), consequently, despite their smaller mean size, the species may attain higher percent cover than *D. johansenii*, which is restricted to patchily distributed substrate within a site. If *D. johansenii* cover is calculated in terms of available log surface area within a site rather than total site area, then average percent cover of *D. johansenii* (0.05%) is more comparable to *D. rigidulus* cover (Table 2.5).

Mnium arizonicum and *M. spinulosum.*—On average, *M. arizonicum* colonies are larger than *M. spinulosum* (Table 2.5, $p<0.001$). *Mnium spinulosum* has higher colony density and mean site percent cover because *M. arizonicum* colonies tend to be more clumped on the landscape with increased colony density beneath sub-alpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) clumps. Average percent cover of *M. arizonicum* within a tree clump is 0.02% versus the overall site coverage of 0.0006%.

Summary.—Considering all six species together, *B. pseudotriquetrum* and *M. macrocarpa* have the highest local abundance, *M. spinulosum* and *D. rigidulus* var. *gracilis* are in the mid-range, and *D. johansenii* and *M. arizonicum* have low local abundance (Table 2.5). The division of species by local abundance relates to the scale of habitat versus site. For *B. pseudotriquetrum*, *M. macrocarpa* and *D. rigidulus* var. *gracilis* the habitat scale is equivalent to the site scale and these mosses achieve relatively higher percent cover within smaller site areas. For *D. johansenii* and *M. arizonicum* there is the largest discrepancy between habitat and site scale. For these two mosses habitat occurs in discrete patches within a site. The discontinuity of habitat means a larger area is required to encounter a given number of colonies and overall percent cover is quite low (Table 2.5), although percent cover on suitable habitat itself is comparable to the other species. Based on site area estimates given in Table 2.5, *M. spinulosum* habitat occurs on the largest continuous scale in Alberta, while *M. macrocarpa* is the most restricted.

Habitat specificity of species.

I view habitat specificity as a pattern of species' occurrence on the landscape and as such, this pattern may or may not reflect a habitat limitation. If habitat specificity does correspond to habitat limitation, then it may take the form of environmental and/or substrate limitations. Substrate specificity may be a more common form of habitat specificity in bryophytes than environmental limitations (Bates 1992, Heegaard & Hangelbroek 1999). Mosses occur on a wide range of substrates including rock (saxicolous), logs (epixylic), trees (epiphytic) and soil (terricolous) (Smith 1982). Qualitative habitat data for each species is summarized from the literature and herbarium specimen labels (Table 2.6). Then I use environment and substrate data to explore differences in the habitat specificity of the study species and the relative importance of abiotic environment versus substrate components of habitat for separating realized habitat space of a species relative to one another (Table 2.6, 2.7; Figure 2.5). In particular, the relationship of habitat parameters to species occurrence is considered.

General habitat descriptions.

Mielichhoferia macrocarpa and *B. pseudotriquetrum.*— *Mielichhoferia macrocarpa* has been observed to grow only "in places where water percolates down from above, or where water splashes up from below" (Brassard & Hedderson 1983). This is true for all sites I have seen during the growing season; however, my study sites become dry seasonally when water at the sites is frozen (i.e., usually November to late June). At the Alberta study sites, it occurs on silt in cracks of calcareous conglomerate, limestone, and shale. Despite the observation of Shacklette (1967) that the species was found only on substrates with greater than average concentrations of heavy metals, the bulk of collection information does not support such a substrate restriction. The substrates reported in herbarium collections encompass many rock types, although they tend to be calcareous (Brassard & Hedderson 1983; pers. obs.). *Mielichhoferia macrocarpa* has been collected from mainly montane areas on limestone, basalt, sandstone and shale (Brassard & Hedderson 1983). *Bryum pseudotriquetrum* grows on mainly basic soils in many habitats (e.g., stream banks, rock cliffs, lakeshores, and fens)

Table 2.6. Qualitative habitat specificity of six study species from literature reports and field observations. Rare species abbreviations are in bold. For the rank sum the lowest possible rank is 2 and the highest is 12.

Species	Substrates	# substrates (rank)	Habitats	# habitats (rank)	Rank sum (overall rank)
Mmac	basic rock	1 (1)	dripping cliffs	1 (1)	2 (1)
Bpse	basic rock & soil, acidic soil	3 (3.5)	stream banks, rock cliffs, lakeshores, fens, ditches	5 (6)	9.5 (4)
Djoh	basic rock, trees, logs	3 (3.5)	arctic tundra, alpine, white spruce floodplains	3 (4)	7.5 (3)
Drig	basic soil & rock	2 (2)	grassland, montane	2 (2.5)	4.5 (2)
Mari	acid & basic soil, tree roots, basic & acidic rock	5 (5)	alpine, subalpine, arctic tundra, stream banks	4 (5)	10 (5)
Mspi	acid & basic soil, tree roots & bases, logs, basic & acidic rock	6 (6)	boreal coniferous forest, temperate mixed hardwood forest	2 (2.5)	8.5 (4)

and is common in suitable habitats throughout northern North America (Crum & Anderson 1981).

Didymodon johansenii and *D. rigidulus* var. *gracilis.—Didymodon johansenii* is restricted to non-terricolous surfaces with a thin layer of fine calcareous silt (pers. obs., Kucera 2000, Pilous 1995, Steere 1978). In the majority of *D. johansenii*'s range these surfaces are rocks; however, in Alberta these surfaces are mainly logs and tree bases (pers. obs., D. Vitt pers. comm.), although it has also been collected on rock in the province (Banff National Park, Crum 1965). *Didymodon rigidulus* var. *gracilis* occurs on calcareous soil in exposed grassland sites, especially over limestone outcrops (pers. obs.). Zander (1981) lists the habitat as also including gravel, sandstone, walls and banks.

Mnium arizonicum and *M. spinulosum.—Mnium arizonicum* is known from alpine and subalpine sites on humus and soil (Koponen 1972, Lawton 1971). Koponen (1972) also notes the occurrence of *M. arizonicum* by woodland streams or on rock cliffs at lower elevations. *Mnium spinulosum* is found on decaying wood, humus and soil in closed-canopy spruce-fir stands (Crum & Anderson 1981, Lawton 1971). However, it may also occur on boulders, rock cliffs and tree bases (Crum & Anderson 1981). Steere (1978) describes *M. spinulosum* as a "characteristic moss of boreal coniferous forest" that does not extend into treeless areas at high elevation or latitudes.

Summary.—Habitat specificity for mosses encompasses both habitat and substrate specificity. Considering the number of substrates that the species occur on, the most substrate specific species are *M. macrocarpa* and *D. rigidulus* var. *gracilis* that only grow on one substrate type (Table 2.6). When habitat specificity is also accounted for, *M. macrocarpa* and *D. rigidulus* var. *gracilis* are still the most specific species (Table 2.6). As a group, the rare study species are not more qualitatively habitat specific than the common study species.

Habitat measurements at study sites.

Habitat variables were measured at the colony scale within five sites for each species (sites are detailed in Table 2.3). These measurements included both environment (light, temperature, moisture) and substrate (pH, organic matter content) variables.

Methods for environmental measurements and substrate measures, i.e., pH and organic matter content, are described in Chapter 3. All environmental measurements, i.e., light, temperature and moisture, analyzed in this section were collected from May to September 1998. Light and moisture were measured at ten-day intervals throughout the growing season and totals for the season were used in the analysis. Methods for light and temperature measurements are identical to those described for the *D. johansenii* experiment in Chapter 4 (light methods also in Chapter 5). Moisture measurements were done using sponges described in Chapter 5 for the 1998 field season when sponges were left *in situ* and weighed in the field every 10 days. The sponges provided an inexpensive method for estimating relative moisture content of moss colonies in the field.

Principal Components Analysis (PCA) was used to analyze the placement of species' sites in environmental space. PCA assumes a linear rather than unimodal relationship between species sites and habitat variables (Jongman *et al.* 1987). PCA was run in PC-ORD, version 4 with correlation cross-products matrix to center and standardize the environmental variables (McCune & Mefford 1999). Standardization was necessary since environmental variables were measured in different units (Jongman *et al.* 1987).

Broken-stick eigenvalues and cumulative correlation coefficients were used to determine which axes were worth interpreting (Table 2.7, McCune & Mefford 1999). Only the two first axes were considered and together these axes explained 78.2% of the variation between species sites (Table 2.7). The first axis (49.1% of variation) is correlated with both a pH-percent organic matter substrate gradient and a temperature-light environmental gradient (Table 2.7). The existence of these gradients is confirmed by the correlation matrix where light was highly, positively correlated to temperature (0.8315) and pH is highly, negatively correlated to organic matter content (-0.8353). The second axis (29.14% of variation) is positively correlated with moisture (Table 2.7).

Within species-pair comparisons for differences in the mean values for environmental variables were made using the Mann Whitney U test, and differences in the range of environmental variables experienced at a given species' sites were compared

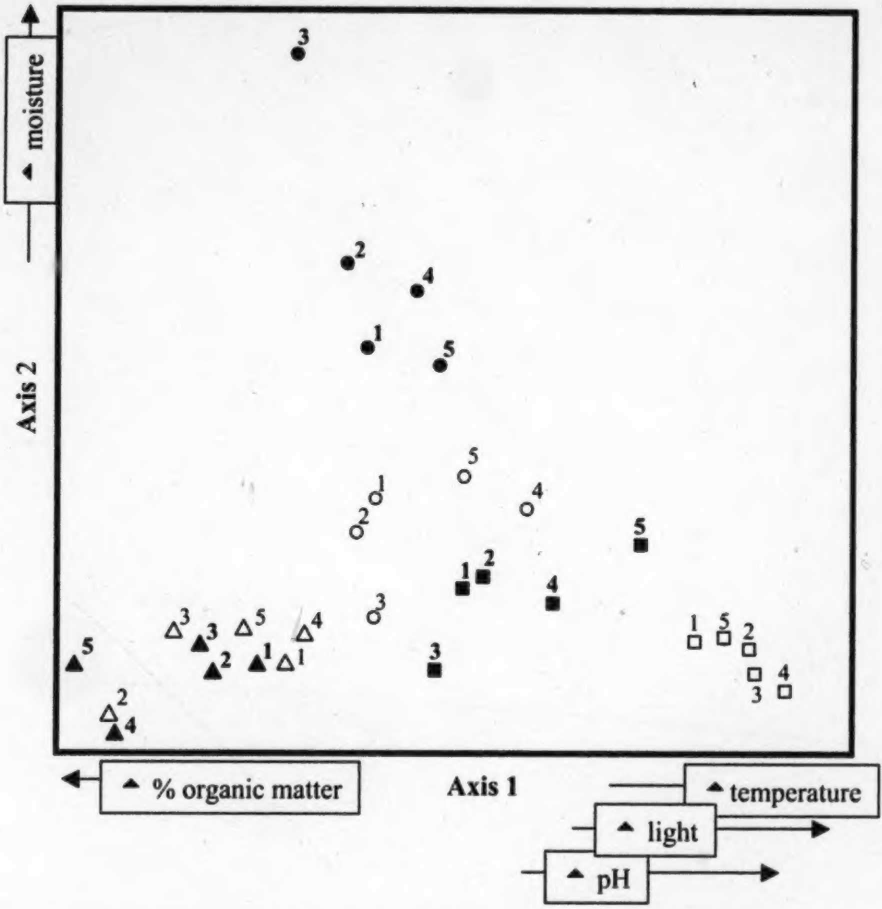


Figure 2.5. Standardized PCA ordination of five habitat parameters at five study sites for each of the six study species showing the first two axes. Substrate pH, percent organic matter, light and temperature are all correlated to Axis 1 and Axis 2 represents moisture gradient. Site symbols are species specific: ● *M. macrocarpa*, ○ *B. pseudotriquetrum*, ■ *D. johansenii*, □ *D. rigidulus* var. *gracilis*, ▲ *M. arizonicum*, and △ *M. spinulosum*. Numbers given beside the species symbols correspond to site names given in Table 2.3.

Table 2.7. Statistics of standardized PCA analysis of species sites in environmental space shown in Figure 2.5. Only five of the six environmental variables were correlated to the significant axes of the ordination, therefore rainfall is not included here.

a. Statistics for the first three axes indicating that only the first two axes of the PCA were significant, i.e. note based on the broken-stick eigenvalue the third axis did not explain more of the variation than would be expected by chance.

Axis	Eigenvalue	% of variance	Broken-stick eigenvalue	cumulative % of variance
1	2.945	49.077	2.450	49.077
2	1.748	29.137	1.450	78.214
3	0.847	14.110	0.950	92.725

b. Correlation of environmental variables (Pearson's r) to the first two ordination axes.

Environmental variable	Axis 1	Axis 2
Light	+0.805	+0.386
Moisture	+0.196	+0.919
Temperature	+0.830	+0.448
pH	+0.770	-0.555
% organic content	-0.800	+0.491

by the variance-ratio test (Table 2.8). A Wilcoxon signed rank test was used to detect significant overall differences between rare and common study species' habitats.

Mielichhoferia macrocarpa and *B. pseudotriquetrum*.—These two species separate from the other species sites mainly along the moisture gradient, axis 2 (Figure 2.5). *Mielichhoferia macrocarpa* sites are significantly darker, colder and wetter than *B. pseudotriquetrum* sites and also have marginally higher mean pH (Table 2.8). Fluctuation of temperature is significantly less at *Mielichhoferia* sites than at *Bryum* sites (Table 2.7). *Mielichhoferia* sites have more variation in moisture because of higher extreme moisture values.

Didymodon johansenii and *D. rigidulus* var. *gracilis*.—The *Didymodon* species occur in some of the hottest, brightest sites (Figure 2.5). *Didymodon rigidulus* var. *gracilis* occurs at significantly brighter, hotter sites with higher soil pH, and lower percent organic matter than *D. johansenii* (Table 2.8). *Didymodon rigidulus* var. *gracilis* also has significantly less variation in substrate pH and percent organic matter content between sites.

Mnium arizonicum and *M. spinulosum*.—*Mnium* sites have higher percent organic matter in their substrates than the other species (Figure 2.5). *Mnium arizonicum* and *M. spinulosum* sites only differ significantly in the lower average temperature at *M. arizonicum* sites over the growing season (Table 2.8). This is unsurprising since *M. arizonicum* sites are located at elevations 600m higher than *M. spinulosum* sites. The two species of *Mnium* do not have any significant differences in the range of environmental variables encountered at their sites. Overall, the *Mnium* habitats are most similar to one another (Figure 2.5, Table 2.8).

Summary.—Within the measured sites, the rare *M. macrocarpa* and the common *D. rigidulus* var. *gracilis* are quantitatively more habitat specific than their partner species, while the *Mnium* species do not differ in their relative habitat specificity. *Mielichhoferia macrocarpa* is mainly more specific (i.e., significantly smaller variance between sites) for environmental variables, while *D. rigidulus* var. *gracilis* is more specific for substrate variables (Table 2.8). The rare study species are not consistently more habitat specific than the common study species.

Table 2.8. Habitat parameters measured in 1998 growing season for six moss species.

a. Light, temperature, moisture and substrate pH and percent organic matter summarized as median with the range in parentheses for three environmental and two substrate variables at five sites per species.

Species	**Light** (sum of exposed photo papers)	**Temperature** (rotation angle of sucrose solution)	**Moisture** (mean grams water gained in 70 days)	**pH**	**% organic matter**
Mmac	26.67	23.19	16.53	8.60	11.10
	(7.68)	(0.36)	(28.72)	(0.46)	(27.36)
Bpse	36.98	17.82	7.18	8.36	53.07
	(6.68)	(9.05)	(4.26)	(1.15)	(61.71)
Djoh	32.46	11.98	2.63	7.98	28.65
	(4.99)	(6.54)	(3.14)	(1.03)	(55.92)
Drig	49.48	0.89	0.61	8.60	6.83
	(10.55)	(6.74)	(5.95)	(0.36)	(3.13)
Mari	28.98	20.27	2.23	5.90	85.92
	(3.46)	(2.76)	(5.68)	(1.51)	(25.60)
Mspi	28.18	2.41	3.56	6.40	85.21
	(5.23)	(2.41)	(2.49)	(1.66)	(56.37)

b. Within species pair comparisons of the means and variance for five environmental parameters. Mean comparisons are Mann-Whitney U tests (first row) and variance or environmental breadth by variance ratio tests (second row). Significance levels: ns, p>0.05, * p<0.05, ** p<0.01.

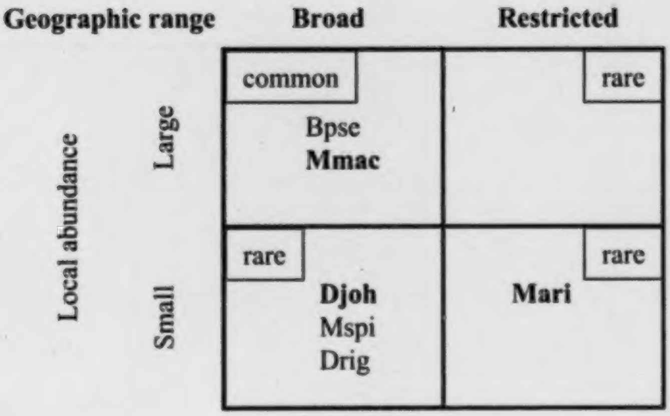
Species pair	Light	Temperature	Moisture	pH	% organic matter
Mmac-Bpse	**	**	*	*	ns
	ns	*	*	ns	ns
Djoh-Drig	**	**	ns	**	**
	ns	ns	ns	*	*
Mari-Mspi	ns	**	ns	ns	ns
	ns	ns	ns	ns	ns

Species pairs are consistently adjacent to one another in the PCA ordination demonstrating that species within pairs have similar habitats (Fig. 2.5). *Mnium arizonicum* and *M. spinulosum* have the greatest habitat overlap of any of the study species (Fig. 2.5, Table 2.8). *Mielichhoferia macrocarpa* separates out most strongly along the moisture axis with much higher moisture than other species habitats. *Bryum pseudotriquetrum* sites have the second highest moisture levels of the species. *Didymodon rigidulus* var. *gracilis* occurs on the most basic, mineral substrates in the brightest, hottest environments. Overall, the rare study species occur at colder, darker sites than the common study species (Fig. 2.5, Wilcoxon signed rank, df = 13, p = 0.005 for light; 0.001 for temperature).

Species in relation to rare-common categories.

When the species are placed into the four categories formed by axes of geographic range and local abundance, the three common species are not all classified as "common" (*sensu* Gleason 1924) with broad geographic range and large local abundance (Fig. 2.6). Two of the common species, *M. spinulosum* and *D. rigidulus* var. *gracilis*, fall into a category often regarded as a type of rarity, i.e. broad geographic range with small local abundance, while *M. macrocarpa*, a rare study species, falls into the one common category (Fig. 2.6). When the parameter of habitat specificity is added to yield the eight categories of Rabinowitz (1981), then only *B. pseudotriquetrum* remains "common" (Fig. 2.7). The only other study to place bryophyte species into the categories of Rabinowitz (1981) similarly found that only 6.7% of the British bryophyte flora was common (Birks *et al.* 1998). The lower percentage of common species for bryophytes is largely attributed to the greater prevalence of habitat specificity in bryophytes (Birks *et al.* 1998).

In addition, I argue that quantifying geographic range as "small" or "large" for land plants as a whole is also problematic because bryophytes tend to have broad geographic ranges and frequent disjunctions (Miller 1982). As discussed in Chapter 1, we may need to quantify concepts such as "narrow habitat specificity" and "small range size" differently for different taxonomic groups because of differences in their overall lineage ages and ecology. The placement of *M. macrocarpa* in Figure 2.6 illustrates this



Local abundance \ Geographic range	Broad	Restricted
Large	common Bpse **Mmac**	rare
Small	rare **Djoh** Mspi Drig	rare **Mari**

Figure 2.6. Study species classification by geographic range size and local abundance. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are in bold typeface.

Geographic range		**Broad**		**Restricted**	
Habitat specificity		*Wide*	*Narrow*	*Wide*	*Narrow*
Local abundance	Large	common Bpse	rare **Mmac**	rare	rare
	Small	rare Mspi	rare **Djoh** Drig	rare **Mari**	rare

Figure 2.7. Study species classification into the eight categories of Rabinowitz (1981) based on geographic range, local abundance and habitat specificity. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are bolded.

point well. As a species with only 23 known localities of occurrence on the planet, *M. macrocarpa* is certainly not common. However, where it does occur it is in high abundance at disjunct locations that cover a broad geographic range.

To attain the rarity scores presented in Figure 2.8, I summed species' ranks for two components each of geographic range (Table 2.2), local abundance (Table 2.5), and habitat specificity (Table 2.6). Ranks were assigned relative to all the other species and the characteristic associated with rarity was always given the lowest rank (1). The highest rank was always 6 and tied species were assigned the same score, i.e., the mean of their rank positions. Ranks were totaled and each species placed on a gradient based on their total score (Figure 2.8). The gradient extends from a low score of six (i.e., rank of one for all six variables) to a high score of 36 (Figure 2.8). On the gradient, the species within rare-common species pairs vary in their separation from one another, although the common species of the pair is always closer to the common end of the gradient. *Mielichhoferia macrocarpa* and *B. pseudotriquetrum* have the largest separation, while the *Didymodon*s are closest (Figure 2.8). The rare *M. arizonicum* is nearer the common end of the gradient than common *D. rigidulus* var. *gracilis*, although this may be an artifact of lack of documentation for *D. rigidulus* var. *gracilis*.

Reproductive potential.

Longton (1992) found that rare moss species were more less likely to produce sporophytes than common moss species in the British flora. Since spores are thought to be the main means of long distance dispersal in mosses, this implies that rare species may be not only reproduction limited, but also dispersal limited. In this section, I mainly address reproductive potential, although dispersal potential is covered briefly under sexual reproductive potential. Little is known about asexual dispersal potential in mosses (Dalen & Söderström 1999) and I will address this topic experimentally in Chapter 5. Reproductive potential as defined here includes sexual and asexual reproduction because although not all six study species produce sporophytes in the study area, all the species are capable of asexual reproduction from gametophyte fragments (pers. obs.). In addition, asexual reproduction from fragments is usually more successful than growth

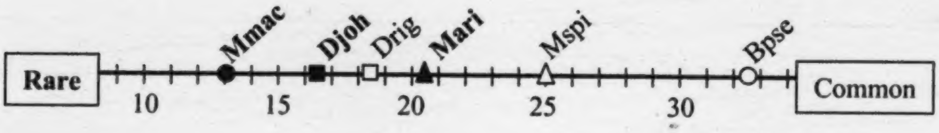


Figure 2.8. Position of six moss species along a rare-common gradient, see text for scoring details. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species abbreviations are in bold typeface.

from spores in the field (Miles & Longton 1990, Newton & Mishler 1994) and this was true for *M. macrocarpa*, *M. arizonicum*, and *M. spinulosum* that all grew from fragments but not spores in field establishment plots (unpublished data). Establishment experiments in this thesis were conducted using gametophyte fragments.

Sexual reproductive potential.

Sexual reproductive potentials of the species are summarized from the literature. I considered sexuality, sporophyte frequency, mean spore size and mean seta length for each species. Spore size and seta length are two sporophyte traits associated with dispersal ability of the spores. Small spores (<25μm) are thought to travel longer distances and a longer seta allows spores to enter the turbulent layer above the boundary layer of the moss colony (Hedderson & Longton 1995). In addition to literature background, sporophyte frequency for the species in the study area is expressed as the percentage of mapped colonies with sporophytes at three sites per species colony mapping data (methods described in this chapter under *Local abundance*).

Mielichhoferia macrocarpa and *B. pseudotriquetrum.*—Despite its dioicy, *M. macrocarpa* produces sporophytes in most populations (Table 2.9, Brassard & Hedderson 1983). Sporophytes occurred on 10.7% of the mapped colonies with high variation between sites (Table 2.9). *Bryum pseudotriquetrum* is reported as dioicous or synoicous (Crum & Anderson 1981) and the sporophyte frequency varies between populations and perhaps between habitats (pers. obs., Lewis-Smith 1999). The populations used in this study grew along mountain stream banks, which experience frequent flood disturbance, and sporophytes were extremely rare to absent throughout the study area. None of the mapped colonies had sporophytes (Table 2.9).

Although sporophyte frequency is lower for *B. pseudotriquetrum* than *M. macrocarpa* in my study area, *B. pseudotriquetrum* sporophytes possess both smaller spores and longer seta than *M. macrocarpa* (Table 2.9). Both of these sporophyte traits are associated with greater dispersal potential (Hedderson & Longton 1995) and so despite its lower frequency of sporophyte production, *B. pseudotriquetrum* may be more efficient than *M. macrocarpa* at sexual reproduction when it does occur.

Table 2.9. Summary of sexual reproduction in six study species. Sporophyte production descriptions specific to the study area are in bold. Rankings are given for sporophyte frequency throughout the species range and frequency within the study area is given in parentheses. Data for sporophyte frequency comes from 50 mapped colonies at 3 sites for each species. Mean spore size and seta length are from Crum & Anderson (1981) for *B. pseudotriquetrum*, *D. rigidulus* and *M. spinulosum* and from Lawton (1971) for *M. macrocarpa*, *D. johansenii* and *M. arizonicum*.

Species	Sex	Sporophyte production		Mean # colonies with sporophytes per 150 (std. dev)	Mean spore size (μm)	Mean seta length (mm)
		Description	Ranking			
Mmac	dioicous	**frequent**	4 (4)	16 (20)	17.5	6
Bpse	monoicous	**rare** – frequent	4 (2)	0	13.5	50
Djoh	dioicous	none – **frequent**	2 (4)	15 (4)	12.5	7.5
Drig	dioicous	**none** – rare	2 (0)	0	12.0	9.0
Mari	dioicous	**none – rare**	1 (1)	0	16.5	18
Mspi	monoicous	**frequent**	5 (5)	56 (15)	20	25

Didymodon johansenii and *D. rigidulus* var. *gracilis.—Didymodon johansenii* is dioicous and, globally, has only been known to produce sporophytes in Alberta. In my study populations, sporophytes occur on about 10% of the colonies (Table 2.9). The lack of sporophyte production in more northerly populations seems curious considering that several collectors have noted the presence of archegonia in these populations (e.g., Williams 1921, Kuc 1973). Whether the majority of the populations are composed only of female plants or whether sporophyte production is prevented by environmental factors varying among these locations remains an intriguing area for experimentation. *Didymodon rigidulus* var. *gracilis* does not produce sporophytes in my study area (Table 2.9) and is reported as very rare throughout its range (R. Zander pers. comm.). When sporophytes do occur they are similar in spore size and seta length to *D. johansenii* (Table 2.9).

Mnium arizonicum and *M. spinulosum.—Mnium arizonicum* is dioicous and sporophyte production is extremely rare (Lawton 1971, pers. obs.). None of the herbarium specimens of *M. arizonicum* in ALTA has sporophytes and, despite the proximity of male and female plants at several study sites, sporophytes were observed in the field only once. On this occasion, the sporophytes still did not contribute to reproduction because the sporangia were consumed by herbivores before spore release (pers. obs.). *Mnium spinulosum* is paroicous (synoicous) and sporophyte production is frequent and prolific (Crum & Anderson 1981). *Mnium spinulosum* is the only study species that is often polysetous, producing more than one sporophyte per gametophyte. *Mnium spinulosum* is reported as having larger spores and a longer seta than *M. arizonicum* (Table 2.9), but these differences are not likely to be important considering the rarity of successful sporophyte production and spore dispersal in *M. arizonicum*.

Summary.—In contrast to the lower proportion of sporophyte production in British rare mosses (Longton 1992), only one of my rare species, *M. arizonicum*, has lower sporophyte production than its common pair. Using sporophyte frequency as the best proxy for sexual reproductive potential, the species rank from least to greatest sexual reproductive potential as: *D. rigidulus* var. *gracilis*, *M. arizonicum*, *D. johansenii*, *B.*

pseudotriquetrum, *M. macrocarpa* and *M. spinulosum* (Table 2.9). There are no remarkable differences in species dispersal potential based on available information.

Asexual reproductive potential.

My establishment experiments compare asexual regeneration of the study species over a range of conditions (Chpts. 3, 4 & 6). Throughout the course of my experiments, I have noticed that each species predictably follows its own sequence of events when regenerating asexually from fragments (Table 2.10) and it has impressed me that the details of regeneration have important implications for the rate of establishment by fragments, e.g. a species that can sprout directly from lateral initials will have an advantage over a species that cannot and must rely instead on cell de-differentiation and production of secondary protonema. I describe the steps of asexual regeneration for each species from my observations and summarize asexual reproductive potential from control plots in the field and growth chamber (Table 2.10).

Mielichhoferia macrocarpa and *B. pseudotriquetrum.*—In *M. macrocarpa*, the leaves of the original gametophyte fragment always go chlorotic and then secondary protonema grow out from the red stem. The protonema produces rhizoids and gametophore buds. Direct sprouting from the stem has also been observed, but it is less common than regeneration via secondary protonema (Table 2.10). Evidence for asexual reproduction in the field was provided by one population of genetically homogeneous, male plants found in the study area (Cleavitt unpbl. isozyme data).

Bryum pseudotriquetrum is more aggressive in asexual reproduction than *M. macrocarpa* in that the original fragment usually remains alive and continues to grow both from the apex and through lateral sprouting. Rhizoids and secondary protonema are produced from the stem and leaves (Table 2.10). *Bryum pseudotriquetrum* has a higher percent regeneration than *M. macrocarpa* in control plots in the field and growth chamber (Table 2.10).

Didymodon johansenii and *D. rigidulus* var. *gracilis.*—*Didymodon johansenii* is the only study species with specialized asexual propagules. The species has caducous leaf tips, i.e., tips of the leaves are specialized to fall off and form new plants. During

Table 2.10. Summary of asexual reproduction in six study species including developmental processes, asexual reproduction specialization and mean percent establishment of fragments in control plots from the field and growth chamber. Standard deviations are given in parentheses beside the mean. Percent regeneration measurements from the field are from 5 sites with 3 replicates each and the chamber experiment had 5 replicates on natural substrate.

Species	Usual steps in asexual regeneration	Asexual reproduction specialization	Asexual reproduction (% establishing) Field	Chamber
Mmac	original fragment goes chlorotic, secondary protonemata grow and produce rhizoids and gametophores, direct sprouting from stem uncommon	none	25 (30)	8 (7)
Bpse	original fragment lives & continues to grow, direct sprouting from stem, rhizoids & secondary protonemata	stem apices often fragile	99 (4)	67 (17)
Djoh	original fragment lives & continues to grow, direct sprouting from stem and leaf apices, rhizoids	caducous leaf apices	7 (25)	81 (17)
Drig	original fragment lives & continues to grow, mainly sprouting along stem, rhizoids	stem apices often fragile	72 (25)	99 (2)
Mari	original fragment sometimes chlorotic, sprouts & rhizoids from stem & green leaves	stem apices fragile	89 (11)	100 (0)
Mspi	original fragment usually chlorotic, sprouts & rhizoids from stem only	none	90 (13)	95 (6)

establishment experiments, *D. johansenii* regeneration from fragments usually involves continued growth of the original fragment and production of rhizoids (Table 2.10). Lateral sprouting from the stem may also occur and secondary protonema and gametophore buds are often produced from the leaf costa or tips, especially at the breaking point of the caducous leaf tips, even if the leaf tips have not fallen off. *Didymodon rigidulus* var. *gracilis* usually only produces lateral sprouts from the original fragment and does not grow many rhizoids or secondary protonema (Table 2.10). *Didymodon johansenii* has low regeneration in the field (Table 2.10) and this is likely due to disturbance, since fragment recovery is quite low and regeneration in the chamber (where disturbance is absent) is quite high (Table 2.10). *Didymodon rigidulus* var. *gracilis* has high asexual reproduction both in the field and chamber, although chamber regeneration is again higher for this species (Table 2.10).

Mnium arizonicum and *M. spinulosum.*—Both species tend to produce prolific rhizoids and at least one sprout, but often many sprouts, from the stem. If the leaves do not go chlorotic, then they may later produce secondary protonema. In *M. arizonicum* sprouts also grow from the leaf costa (Table 2.10). *Mnium arizonicum* and *M. spinulosum* both have very high percent regeneration in the field and the growth chamber (Table 2.10).

Summary.—If the overall success of asexual regeneration from fragments is used to rank least to greatest asexual reproductive capacity, then the species are arranged: *M. macrocarpa*, *D. johansenii*, *B. pseudotriquetrum*, *D. rigidulus* var. *gracilis*, *M. spinulosum* and *M. arizonicum* (Table 2.10). *Didymodon rigidulus* var. *gracilis* and *M. arizonicum* rely almost exclusively on asexual propagation.

Reproduction and rarity.

Both sexual and asexual reproductive potential was ranked for the species (Tables 2.9 & 2.10). Species vary in the relative importance of sexual versus asexual reproduction and none of the species ranked exactly the same for both (Tables 2.9 & 2.10). *Bryum pseudotriquetrum*, *D. johansenii* and *M. spinulosum* all had comparable rankings for sexual and asexual reproduction indicating that these three species invest about equally in the two types of reproduction. In contrast, the relative rankings of the other species suggest that *D. rigidulus* var. *gracilis* and *M. arizonicum* rely more on asexual reproduction while *M. macrocarpa* relies more on sexual reproduction. Two of the three rare study species do not conform to general pattern of less sexual reproduction and more asexual reproduction suggested for rare mosses by Longton (1992) and Hedderson (1992).

Conclusions.

Species within pairs are related to one another at the genus level, although the current taxonomy of *M. macrocarpa* does not reflect its close phylogenetic relationship to *B. pseudotriquetrum*. Despite the close relationship of the species, they often differ in plant size and the rare species are characterized by smaller size than their common partners (Figure 2.1). The six study species represent a wide range of rare and common species types (Figures 2.6, 2.7). In terms of geographic distributions, both endemic and widely disjunct distributions are represented by the rare species while the common species vary from cosmopolitan to circumboreal (Table 2.1). The species also vary in colony size and overall local abundance (Table 2.5).

Gaston and Kunin (1997) have suggested that, in general, rare species are more likely to be self-compatible or reproduce asexually, invest less in sexual reproduction, disperse less effectively and use less common and/or a narrower range of resources (see Chapter 1, Table 1.3). In terms of habitat specificity or usage, both rare and common species can have narrow habitat breadths with common species being specific to a widespread habitat (Table 2.8). These three rare species may use habitats that are less common on the landscape than their common partners as suggested by Vitt and Belland (1997) and Hanski *et al*. (1993); however, due to time constraints no attempt was made to quantitatively assess habitat availability on the landscape. Rare species did not consistently have lower reproductive potential than their common species pair and the rare species cover the full range of emphasis on sexual versus asexual reproduction. In my study area, *M. macrocarpa* reproduces mainly sexually, *M. arizonicum* mainly asexually and *D. johansenii* relies about equally on both methods of reproduction.

Comments on dispersal ability are premature given our current knowledge for these species.

Significant trends for rare versus common species in this study are that rare species have lower global frequency and that rare species grow in colder, darker sites than their common species pair. Because broad, disjunct distributions are prevalent among bryophytes, global frequency may be a more practical parameter than global range size for quantitatively delimiting rare from common species. The occurrence of rare species at relatively colder, darker sites suggests that physiological differences may exist between rare and common species. Differences between rare and common species are interesting, but the differences in themselves tell us little about the reasons for these differences. In the next four chapters I present evidence for mechanisms addressing differences in species substrate specificity (Chapters 3 & 4), asexual dispersal and habitat restriction (Chapter 5), and demography and competition (Chapter 6).

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Chapter 3: The role of physiologically based substrate specificity for six species occurring on substrates with varying pH and organic matter content*

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Mosses are renowned for their substrate specificity. For example, some species only occur on high nutrient dung or soils with high heavy metal concentrations. One can also find remarkably different bryophyte species assemblages within close proximity on calcareous and non-calcareous substrates (Bates 1992). Smith (1982) presented results from several studies demonstrating the relationship between bryophyte species assemblages and rock type. In particular, limestone had a more specific flora than non-calcareous rock types (Smith 1982). Similarly, Robinson *et al.* (1989) found the bryophyte and lichen floras of basic soils to have many more unique species than do the acidic soil floras in the Canadian subarctic. In addition, mosses were more substrate specific than terricolous lichens (Robinson *et al.* 1989).

Throughout this paper, "substrate specificity" is used to describe an observed distribution pattern. The term is applied broadly in some places to recognize that most moss species have some level of substrate specificity. However, the concept of substrate breadth, i.e., the range of substrate chemistry for substrates that a species occurs on, is used to distinguish species with narrow or broad specificities.

In tracheophytes, sensitivity to substrate chemistry is linked to limitations on the nutrient uptake ability of plants (Tyler 1994, Tyler & Ström 1995). Lee (1999) reviewed the current knowledge of calcicole-calcifuge substrate limitations and pinpoints cation concentration effects on plasma membrane functioning as central to the habitat limitation. Species that cannot grow on calcareous soils may be inefficient in iron uptake because they lack the efflux mechanisms necessary to prevent buildup of calcium in the cytoplasm. Species that are sensitive to acid soils lack aluminum sequestering mechanisms to prevent a buildup of aluminum on their cation exchangers (Lee 1999). Lee (1999) postulates that these differences in susceptibility to calcium versus aluminum toxicity may result from different ion gate mechanisms in the plasma membranes of these two groups of plants (i.e., calcifuge and calcicole, respectively).

A correlation between substrate preference and cation exchange capacity (CEC) has been documented in mosses. In general, mosses have relatively high CEC because they have cation exchangers over their whole surface (Brown 1982). Bates (1982) found that mosses growing on calcareous rock substrates had even higher CEC than calcifuge species. For forest bryophyte species, Büschner *et al.* (1990) argued that low CEC seems to be essential for taxa adapted to growing on acid (below pH 5.0) soils. A correlation between CEC and degree of substrate specificity is to be expected since CEC has indirect effects on ion concentrations near the cell membrane (Marschner 1986). Büschner *et al.* (1990) suggested that these indirect effects will be most severe for calcicole species exposed to acid soil conditions where the higher concentration of cation exchangers will preferentially bind aluminum over calcium.

Overall, the reasons for calcifuge and calcicole distributions are not as clear in mosses as they are in tracheophytes, partially because atmospheric deposition is thought to be a more important source of nutrients than substrate for mosses (Tamm 1953, Bates 1989, Bates 1993) and partially because, in general, little is known about nutrient uptake in bryophytes (Bates 1992; Lee 1999). Robinson *et al.* (1989) suggested that the paradox of substrate specificity in organisms not thought to take up nutrients directly from their substrate may be explained by indirect effects of substrate chemistry through wind blown particles or through solute concentrations in rain and snow melt. The many studies demonstrating that moss mineral contents reflect substrate chemistry (e.g., Shacklette 1967, Bates 1982, Webster 1987, Ron *et al.* 1999) support the idea that bryophytes may obtain nutrients directly or indirectly from their substrate. In particular, substrates high in elements such as heavy metals or calcium may exert a strong influence over the mineral nutrition of bryophytes growing on them (Brown 1982).

It may also be that some bryophytes do take up nutrients directly from their substrate and that the findings of Tamm (1953) and Bates (1989, 1993) for large pleurocarpous mosses may pertain mainly to that growth form (Bates & Bakken 1998). The relative importance of atmospheric versus substrate contributions to bryophyte mineral nutrition should be more fully evaluated both for different nutrients and for species with different growth forms and substrate preferences (Brown 1982, Bates & Bakken 1998). In addition, topics such as the potential role of rhizoids in translocating nutrients from the substrate remain to be resolved (Brown 1982, Rincon 1990, Bates 1992).

Many authors have pointed out that the relative importance of substrate chemistry may change over the life of the moss and perhaps substrate chemistry is most crucial during the establishment stage (Brown 1982, Robinson *et al.* 1989, Bates & Farmer 1990, Bates 1992, Bates & Bakken 1998). Rincon (1988) investigated the effect of organic litter composition and soil nutrient content during stem fragment regeneration for five bryophyte species. All five species had higher relative growth rate on *Urtica dioica* stem litter and fertilized soil when compared to growth on control plots. However, the four other types of plant litter included in the study did not enhance growth of the bryophytes and this may be due to their lower nutrient value. No other studies have considered the role of organic matter in bryophyte substrate preference, although Brown (1982) highlighted the importance of considering the role of organic matter in bryophyte nutrient acquisition.

In general, upland soils high in organic matter are more acidic than mineral soils due to lower base ion saturation and microbial respiration that results in the formation of carbonic acid in soil solution (Plaster 1997). In addition to influencing pH, organic matter can affect the availability of other ions in solution, potentially provide a nutrient source, and possibly influence plant establishment if growth-affecting chemicals are present (Brown 1982). Substrate texture and water holding capacity also vary with organic matter content (Plaster 1997).

If substrate chemistry is most influential during the establishment stage of a moss, then the substrate specific patterns of moss communities must largely be decided during this stage. Studies from two very different moss habitats both have found evidence for the importance of the regeneration niche (*sensu* Grubb 1977) in structuring bryophyte communities. Kimmerer and Young (1996) found the interaction between disturbance regime and regeneration niche to be the most important factors for influencing community structure on logs in mixed hardwood conifer forest. Li and Vitt (1994, 1995) demonstrated differences in the regeneration niches of five peatland mosses that underline the crucial role of the establishment stage in forming mature peatland bryophyte community patterns.

Even though the mechanisms underlying bryophyte substrate specificity patterns are not clear, the link between substrate specificity and species distributions has been recognized. For instance, wide tolerance for substrate chemistry has been correlated with common or widespread species (see results of Shaw 1981 for *Pohlia* and Horton 1988 for *Encalypta*). Both Shaw (1981) and Horton (1988) found the pH gradient yielded the most distinct species groupings. Often habitat specificity has been invoked as one potential explanation of species rarity (Rabinowitz 1981, Fiedler & Ahouse 1992). As Fiedler and Ahouse (1992) emphasize, in order to make intelligent management decisions for rare species, it is not enough to categorize types of rarity; we also need to understand the factors that are responsible for species rarity. The rather practically oriented definitions of rare and common species used in this paper are based on species' distribution records as detailed in the methods. The observed substrate specificity patterns of a species do not necessarily equate with that species' occurrence being substrate limited since other factors such as competition and dispersal limitation can also control species' occurrence. Therefore, experimental evidence of substrate effects on establishment and growth is required to confirm substrate limitation. In addition, substrate limitation may be physiologically based or may result from physical and disturbance constraints on establishment. This study explores only physiologically based substrate limitation.

Three rare and common moss species pairs were used to compare the role of substrate specificity in physiologically limiting short-term establishment of these species from gametophyte fragments. The six species are all acrocarpous and grow on soils that vary in pH and organic matter content. This comparative approach addresses three questions: 1. Do the rare species occur on a narrower range of substrates than do the closely related common species? 2. Do all species establish significantly better on native substrate (i.e., substrate where the species naturally occurs)? 3. Are some species, such as rare or calcicole species, more sensitive to substrate chemistry during short term establishment?

METHODS

Study species.—Three species pairs were chosen for this study using the following criteria: 1. The species were considered taxonomically sound. 2. Rare species were listed as rare (i.e., S1, five or fewer occurrences or S2, 5-20 occurrences) in Alberta in 1996 when the study was started and were documented in the literature as infrequent throughout North America. 3. Common species were taxonomically closely allied to the rare species and were also documented as widespread throughout North America. The three species pairs, with the rare species listed first, are *Mielichhoferia macrocarpa* (Hook) Jaeg. and *Bryum pseudotriquetrum* (Hedw.) G.M.S., *Didymodon johansenii* (Williams) Crum, and *Didymodon rigidulus* Hedw. var. *gracilis* (Schleich.) Zand., and *Mnium arizonicum* Amann and *Mnium spinulosum* Bruch & Schimp. *Didymodon rigidulus* var. *gracilis* is referred to as *D. rigidulus* throughout the rest of this chapter. All collection sites were located in the eastern front ranges of the Canadian Rocky Mountains, in Jasper National Park and the newly designated Whitehorse Creek Wildland Park of Alberta.

Mielichhoferia macrocarpa is known from three localities in Alberta and twenty localities in North America (Brassard & Hedderson 1983). Note that as used here, a locality may include more than one site if the sites are not more than several kilometers apart, i.e., the sites used here represent one locality in Alberta. The moss has been collected from mainly montane areas on limestone, basalt, sandstone and shale (Brassard & Hedderson 1983) that are constantly moist with seepage or splash. At the Alberta study sites, it occurs on silt in cracks of calcareous conglomerate, limestone, and shale. *Bryum pseudotriquetrum* grows on soil in many circumneutral to basic habitats (e.g., stream banks, rock cliffs, lakeshores, and fens) and is widespread throughout northern North America.

Didymodon johansenii is usually described as a rare Arctic species that grows on calcareous soil (Crum 1965, Zander 1998). It is known from five localities in the montane *Picea glauca* floodplains of Alberta where it occurs on silt-covered logs. *Didymodon rigidulus* is common throughout the North American prairies and into the montane, where it occurs on calcareous soil (Zander 1998).

Mnium arizonicum is known mainly from alpine and subalpine sites on humus and soil; however, Koponen (1972) reported two collections from the Arctic. *Mnium arizonicum* is known from twenty-five localities in Alberta. The common species, *Mnium spinulosum* is found on decaying wood, humus and soil in spruce-fir stands throughout the Boreal Zone of North America.

Substrate organic matter and pH measurements.— A minimum of five sites were selected per species at which 1-3 samples were collected. Substrate samples were collected by removing the colonies of each species and taking the top three cm of substrate directly below the live moss in September of 1998 and 1999 for measures of organic matter content. Substrate samples were frozen for transport to prevent changes in pH from occurring, then thawed and air dried before analysis. Samples were homogenized with a mortar and pestle, and large pebbles and roots were removed from the samples. The portion of each sample to be analysed for percent organic matter was homogenized in a coffee grinder and passed through a 2-mm sieve (Kalra & Maynard 1991). Then these samples were burned for four hours at 550°C (modified from one hour burn used by Dean 1974) and percent organic matter was calculated from loss on ignition. The pH was measured on 1999 samples by making soil slurries in 0.5M $CaCl_2$ at the soil:solution ratio of 1:2 for mineral soil and 1:4 for highly organic soil (Kalra & Maynard 1991). Measurements were taken on a Beckman pH meter standardized with pH 4.0 and 7.0 buffer solutions.

Substrate chemistry samples were averaged by site. Then the mean ranks of species chemistry values were compared using Kruskal-Wallis non-parametric ANOVA and STP post hoc. Non-parametric tests were chosen because of small sample sizes ($n < 6$) resulting from the number of rare species sites available, and not because of obvious deviations from a normal distribution in the data. The variance ratio test for equality of variances was used to look for significant differences in the variance of pH and percent organic matter values between species pairs. Although the variance ratio test is adversely affected by non-normality, it was chosen since non-parametric tests of dispersion are plagued by low power (Zar 1996).

Substrate short term establishment experiment.—Plant material and substrate samples were collected in 1999 at the same time and in the same manner as samples for chemical analysis and were stored in a 4°C refrigerator until planting. Roughly equal numbers of fragments from all populations of a species were mixed and rinsed in double-distilled water. Ten sets of twenty fragments each were then counted from this mixed population pool. The fragments were planted on either native substrate as a control or the opposite of their native substrate for the treatment, that is, a species found on a high pH, low organic matter soil would have an acidic, highly organic treatment (i.e., opposite) substrate. Control (i.e., native) substrates were mixtures made from roughly equal amounts of substrate from each of the five native sites. The treatment substrate of acidic, highly organic soil for calcicole species was a homogenized mixture from the *M. arizonicum* sites. Calcifuge species with a treatment substrate of high pH and low organic matter were planted on a soil mixture from *D. rigidulus* sites.

The fragments were grown in 100 ml clear glass specimen jars for 60 days from November 1999 to January 2000 in a 15°C growth chamber with a 16 hour daylight cycle at an average light intensity of 1,350 lux. The experiment duration and growth conditions were chosen based on these species' regeneration during several preliminary establishment experiments. Fragments were watered with 1–3 ml double distilled water every 15 days if necessary. The clear glass jars were covered with Para film to maintain high humidity while allowing gas exchange to occur. The experiment was a species-by-substrate two-way ANOVA design with five replicates per treatment and twenty fragments per replicate. Results were recorded as proportion of fragments that regenerated, i.e., grew and remained alive throughout the experiment. Growth included growth of rhizoids, gametophyte sprouts, secondary protonema as well as new growth on the original fragment. The number of fragments regenerating specifically by gametophyte sprouting was also recorded. It should be noted that "regeneration" is used in this paper in the sense of fragments being regenerants rather than to refer to a population level phenomenon. Therefore, regeneration and short-term establishment are used interchangeably.

Regeneration and sprouting proportion data were normalized by arcsine square-root transformation and analyzed by two-way species by substrate model I ANOVA and subsequent one-way substrate ANOVAs for each species both calculated by General

Linear Model method using SPSS version 7.5 for Windows. The Tukey HSD post-hoc test was used for determining significant mean separation.

RESULTS

Substrate breadths.— Rare species did not consistently have lower variation in their pH and organic content values than common species. In other words, rare species did not necessarily have narrower substrate breadths than common species, with respect to these factors. *Mielichhoferia macrocarpa* and *D. rigidulus* grew on substrates with a significantly lower organic matter content than all other species except *B. pseudotriquetrum* (Fig. 3.1). *Mielichhoferia macrocarpa* and *D. rigidulus* also had a significantly lower variation in organic matter values than their paired species ($p = 0.05$ and < 0.001, respectively). The *Mnium* species had no significant difference in their substrate organic content variation. *Mnium arizonicum* and *M. spinulosum* were collected from significantly more acidic substrates than the other species with mean (not shown) and median pH values below pH 5.0 (Fig. 3.2). The 1999, pH-$CaCl_2$ measurements indicate that *M. macrocarpa* and *D. rigidulus* have a significantly lower variation in substrate pH values than their pair species ($p = 0.02$ for both). The *Mnium* species had no significant difference in variation of their substrate pH values.

Substrate preferences and establishment ability.—The substrate preferences of the six species in this study could be generalized into three groups based on pH and percent organic matter values: high pH with low organic matter (*M. macrocarpa* and *D. rigidulus*), high pH with broad range of organic matter (*B. pseudotriquetrum* and *D. johansenii*) and low pH with high organic matter (*M. arizonicum* and *M. spinulosum*) (Figs. 3.1 & 3.2).

Overall, species regenerated significantly better on their native versus substrates (two-way ANOVA, $p = 0.001$; Fig. 3.3) as there was not a significant species by substrate interaction. However, in subsequent one-way analysis, only *M. macrocarpa* and *D. rigidulus* had significantly lower regeneration on treatment (i.e., opposite) (Fig. 3.3). *Mielichhoferia macrocarpa* had significantly lower regeneration than did any of the other species both in the control and treatment (Fig. 3.3; Table 3.1). *Mielichhoferia*

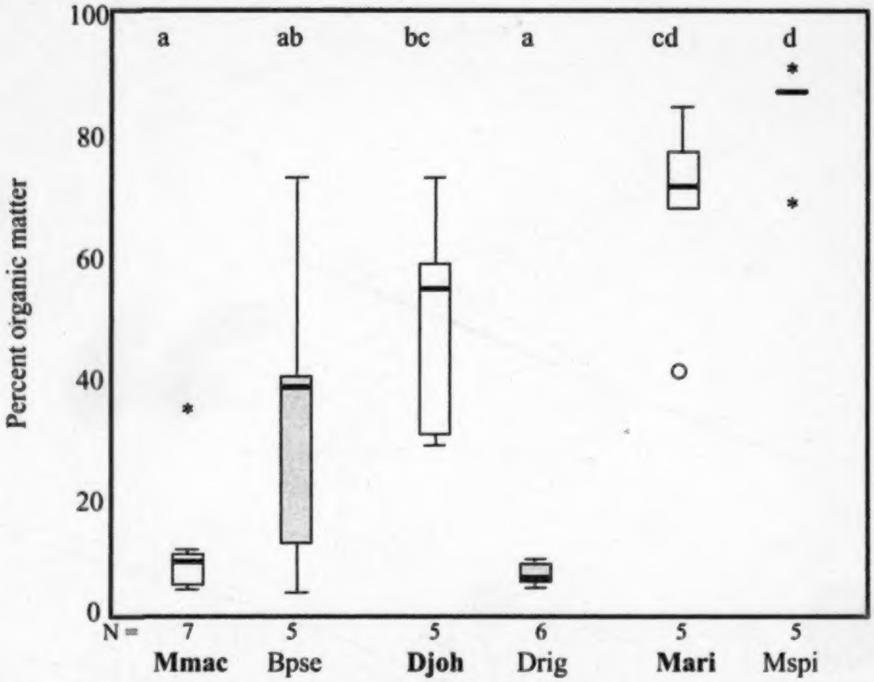

Figure 3.1. Box plot of substrate organic matter content for microhabitats of six moss species from Canadian Rocky Mountain study sites in Alberta. Species' abbreviations are the first letter of the genus and first three letters of the specific epithet and rare species are in bold and to the left of their common congener. The number of sites sampled for each species is given directly above the species abbreviation. Matching lower case letters denote homogeneous subsets from STP post-hoc analysis of Kruskal-Wallis test. Horizontal line represents the median value while the box around it shows the spread of 50% of the data. Vertical bars from the box give the interquartile range (80 % of the data). Circles indicate outliers (data values beyond 3 interquartiles). Asterisks denote extreme values.

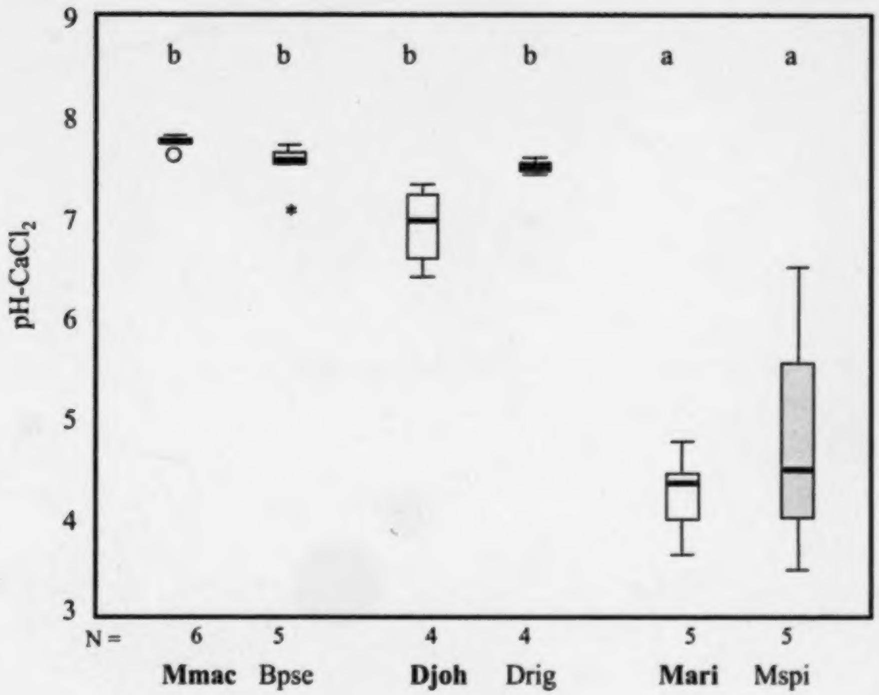

Figure 3.2. Box plot of substrate pH-CaCl$_2$ values for microhabitats of six moss species from Canadian Rocky Mountain study sites in Alberta. Species' abbreviations are the first letter of the genus and first three letters of the specific epithet and rare species are in bold and to the left of their common congener. The number of sites sampled for each species is given directly above the species abbreviation. Matching lower case letters abbreviations denote homogeneous subsets from STP post-hoc analysis of Kruskal-Wallis test. For explanation of box plot refer to Figure 3.1.

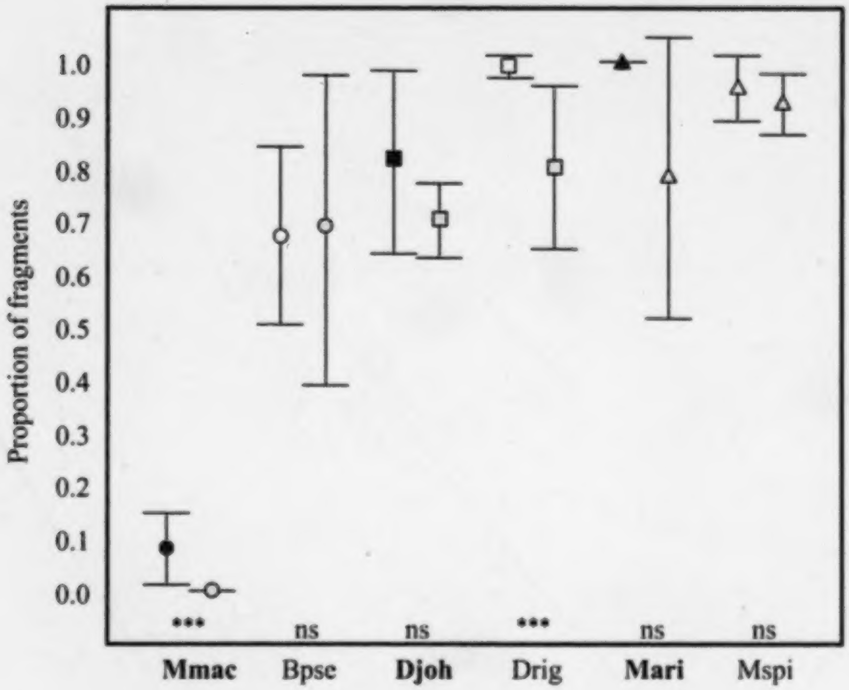

Figure 3.3. Comparison of species overall regeneration on control and treatment substrates. Species' abbreviations are the first letter of the genus and the first three letters of the specific epithet. Control substrates are species native substrates and are indicated by symbols in black (rare species and white (common species). Treatment substrate is a substrate with the opposite extreme of pH and percent organic matter and is indicated by the gray symbols(see text for further details). Error bars represent one standard deviation. The significance of treatment effect by one-way ANOVA is indicated by: ns, p>0.05, *, p<0.05, **, p<0.01, ***, p < 0.001.

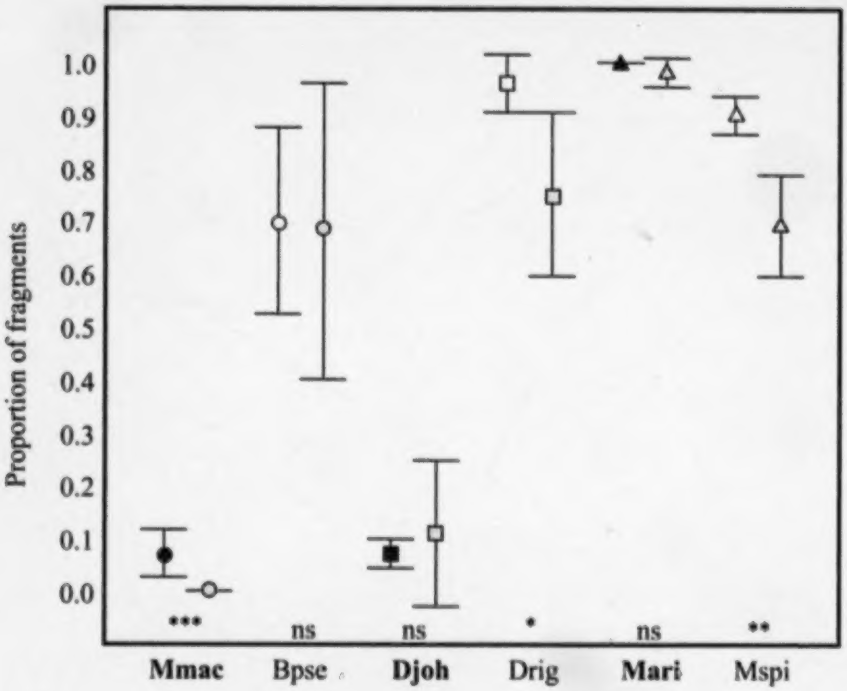

Figure 3.4. Comparison of species regeneration by sprouting on control and treatment substrates. Species' abbreviations are the first letter of the genus and the first three letters of the specific epithet. Control substrates are species native substrates and are indicated by symbols in black (rare species and white (common species). Treatment substrate is a substrate with the opposite extreme of pH and percent organic matter and is indicated by the gray symbols (see test for further details). Error bars represent one standard deviation. The significance of treatment effect by one-way ANOVA is indicated by: ns, $p>0.05$, *, $p<0.05$, **, $p<0.01$, ***, $p < 0.001$.

Table 3.1. Summary of species establishment shown in Figures 3.3 and 3.4. Actual proportions of fragments alive with growth are shown in Figure 3.3 and the proportion of fragments with sprouts is shown in Figure 3.4. This summary is based on homogeneous subsets from Tukey HSD post-hoc analysis with species having the lowest proportion of fragments alive or sprouting designated by "a". Species abbreviations are the first letter of the genus and first three letters of the specific epithet. Homogeneous subsets (i.e., subsets composed of species for which there was no significant difference in establishment) are denoted by species that share the same letters. Species are listed in order of increasing regeneration. Rare species are indicated by bold typeface.

Substrate	**Parameter**	**Species order with respective post hoc subsets**					
Native (control)	Alive w/growth	**Mmac**	Bspe	**Djoh**	Mspi	Drig	**Mari**
		a	b	bc	cd	d	d
	Sprouts	**Mmac**	**Djoh**	Bspe	Mspi	Drig	**Mari**
		a	a	b	c	cd	d
Opposite (treatment)	Alive w/growth	**Mmac**	**Djoh**	Bspe	Drig	**Mari**	Mspi
		a	b	b	b	b	b
	Sprouts	**Mmac**	**Djoh**	Mspi	Bpse	Drig	**Mari**
		a	a	b	b	b	c

macrocarpa and *Didymodon johansenii* both regenerated significantly less by sprouting than the other species (Table 3.1, Fig. 3.4).

Rare and calcicole and substrate sensitivity.—The only group of species to show significant substrate effects on regeneration were the calcicole species that normally grow on substrates low in organic matter (i.e., *M. macrocarpa* and *D. rigidulus*) (Table 3.1, Fig. 3.3). There was no trend for the three rare species, although *M. macrocarpa* and *D. johansenii* tended to have lower overall establishment than their common species' pairs (Fig. 3.3). *Mielichhoferia macrocarpa*, *M. spinulosum* and *D. rigidulus* all had significantly fewer plants regenerate by sprouting on the opposite versus control substrates (Fig. 3.4).

DISCUSSION

Substrate breadths.—In this study, there was no link between rarity and the degree of substrate specificity. Only one of the rare species, *M. macrocarpa*, had a narrower substrate breadth than its paired common species. The *Mnium* pair did not have significantly different substrate breadths for either pH or organic content. The common species, *Didymodon rigidulus*, had a narrower substrate breadth than the rare *D. johansenii*. This last result was particularly unexpected because *D. johansenii* has been considered substrate specific and a calcicole (Crum 1965, Kuc 1973).

The *Didymodon* species demonstrate that the definition of "common" used in this study disagrees somewhat with the concept used for vascular plants by Rabinowitz (1981). Rabinowitz's (1981) classification would require any habitat specific plant to be considered a type of rare plant. Birks *et al.* (1998) report that 77.2% of British mosses are habitat specific and only 6.7% of the British moss flora would be classified as common species under Rabinowitz's topology. However, just as Rabinowitz's classification emphasized that being rare was not a monolithic category, the species in this study demonstrate that being common is also not monolithic, that is, there is also more than one way to be common. In bryophytes, it is possible to have a common species that is habitat specific for a widespread, common habitat. Recognition of this difference between bryophytes and vascular plant species should be taken into account when classifying bryophyte species as rare or common.

Substrate preferences and establishment ability.—The overall higher establishment on native substrate suggests that observed substrate preferences in the field have some physiological basis. However, four of the species did not establish significantly better on native substrate when the results were analyzed separately for each species (Fig. 3.3). These four species either may not be substrate limited or may be limited by substrate in some way that is not primarily physiologically based. Another explanation would be that the potentially detrimental effects of the substrate treatment on these species were of a chronic nature and would require longer than 60 days to manifest as decreased regeneration. For instance, although there was no significant decline in regeneration on treatment soil for the *Mnium* species, both species were beginning to show chlorophyll loss (more pale coloration) on a few plants in the calcareous substrate treatment by the end of the experiment. *Mnium spinulosum* also produced significantly fewer plants with sprouts on the opposite than on the native substrate. This decrease in sprout production indicates that the calcareous mineral soil presented less favorable growing conditions that did not allow *M. spinulosum* to increase its gametophyte biomass (Fig. 3.4). It is unclear whether these negative effects of substrate treatment on *Mnium* regeneration would have been fatal and whether the visible damage was the result of toxicity or nutrient deficiency. It would be useful to separate the effects of pH from percent organic matter in future experiments. In addition, the high humidity and constant environment of the growth chamber may have masked substrate and environment interactions relevant to a field situation. A long-term field experiment with an array of substrate plots in the species' native habitats would be an excellent method for delving deeper into possible species' substrate limitations.

Rare species' substrate sensitivity.—The lack of correspondence between substrate breadth and rarity mirrors the lack of correspondence between substrate sensitivity and rarity. In other words, rare species were not more likely to be physiologically limited by substrate than common species. In this study, rare-common species differences were not as strongly substrate based as was suggested by the data of Shaw (1981) for *Pohlia* and Horton (1988) for *Encalypta*.

The significance of substrate limitations is difficult to assess and requires consideration of other possible limiting factors. *Mielichhoferia macrocarpa* and *D. rigidulus* are certainly limited *to* calcareous substrates, but whether they are limited *by* these substrates remains unresolved. Using unpublished evidence for *M. macrocarpa* to elaborate this point, establishment experiments at suitable, but, as yet, unoccupied field sites indicate that dispersal may also limit *M. macrocarpa*. In addition, plot data comparing attributes of suitable occupied and unoccupied sites shows that the species is absent from sites with higher percent cover of other moss species and implicates competition as a third possible limiting factor for *M. macrocarpa*.

The consistently lower establishment of *M. macrocarpa* and *D. johansenii* relative to their common congeners contrasts with the similarity between the *Mnium* species' establishment abilities. This similarity indicates that *M. arizonicum*'s restricted distribution is not the result of poor establishment ability. Furthermore, if we consider that the most practical classification of rare species would create groups based on their limitations (e.g., Rosenzweig & Lomolino 1997), then *M. arizonicum* likely represents a different type of moss rarity than *M. macrocarpa* and *D. johansenii.*

Calcicole species substrate sensitivity.-The sensitivity of two of the calcicoles, *M. macrocarpa* and *D. rigidulus*, in this study supports the suggestion of Büschner *et al.* (1990) that acid conditions may be more immediately harmful to calcicoles than calcareous conditions are to calcifuges. If cell membrane efflux mechanisms are the cause of calcium toxicity in vascular calcifuges, then the reported "leakiness" of bryophytes during dehydration and rehydration cycles (Bates 1989,1992; Bates & Bakken 1998) may mean that these mechanisms are not as important for regulation of cytoplasmic ion concentrations in bryophytes as they are in vascular plants. However, there is evidence of the need for an active calcium efflux mechanism in bryophytes from membrane potential studies, although the transporter has not been characterized (Raven *et al.* 1998).

The absence of a short term substrate effect in the group of calcicole species with a broader range of organic content values, *B. pseudotriquetrum* and *D. johansenii,* suggests that adaptation to a broad tolerance of organic matter contents might coincide with less sensitivity to variability in substrate pH. This idea is further supported by the correspondence between significantly higher variability in pH and percent organic matter of field substrates of these two species relative to their rare species pairs (Figs. 3.1 & 3.2).

Conclusion.

The rapid response of fragments to substrate treatment in this study contrasts with several studies in the literature that found no differences in growth between treatment and control plots for similar experiments (Bates 1989, 1993). However, the latter studies evaluated species' responses using changes in adult transplant biomass for pleurocarpous mosses. The relatively fast response of regenerating fragments to substrate treatment in this experiment supports the widely expressed idea that substrate specificity may exert the most influence over species survival during the establishment stage. In addition, the lack of atmospheric mineral deposition in this experiment suggests that the fragments of these acrocarpous mosses were taking up nutrients and water from the substrate during regeneration. The possible drawbacks of using bryophyte fragments outlined by Brown (1982) seem to be outweighed by the benefits of studying plants during the establishment phase.

Bates and Farmer (1990) suggested that the physiological ties between moss and substrate are stronger in the establishment stage because during this stage the mosses are in direct contact with the substrate and they must acquire the nutrients necessary to increase their biomass. In addition, fragments require rapid initial growth in order to secure themselves to the substrate. This results in a very strong feedback loop during establishment between increased substrate contact and increased stability and biomass.

Regeneration experiments are a very powerful method for exploring the presence or absence of a species' habitat limitation. This information can be particularly crucial for making management decisions about rare species. Regeneration experiments using plant fragments require minimal damage to existing populations while offering both a means of assessing habitat limitation and of propagating rare mosses for re-introduction to sites in the field.

That comprehensive ecological studies must not only describe habitat preferences of species (*sensu* environmental niche (Birks *et al.* 1998) and niche breadth Slack (1990, 1997)), but also test the significance of these habitat preferences experimentally, is not a new idea (e.g., Forman 1964, Grubb 1977). Studies in bryophyte ecology that have included both components conclude that species' distribution patterns partly (Frego & Carleton 1995) or wholly (Alpert 1988, Li & Vitt 1994, 1995, Kimmerer & Young 1996) reflect constraints on establishment. The results of this study once again emphasize the importance of the regeneration niche in bryophyte ecology and further suggest that the responses of moss species to substrate chemistry during establishment may be determining the structure of calcicole communities.

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Chapter 4: A test of physical limitation to specific substrates during establishment for *Didymodon johansenii*, a rare moss*

*A version of this chapter has been accepted for publication in the *Journal of Bryology*

Rare plant species are often habitat specific (Rabinowitz 1981, Fiedler & Ahouse 1992); however, the pattern of habitat specificity does not necessarily equate with the process of habitat limitation. Substrate specificity is one prevalent form of habitat specificity among plants. Substrate specificity patterns may result either from species' substrate limitation (i.e., the species is not capable of growing on other substrates), from factors extrinsic to the substrate itself such as competition (i.e., the species is capable of growing on other substrates, but is prohibited from growing on them), or from a combination of these two factors. It is difficult to decipher which factors actually limit species because habitats encompass many factors including substrate chemistry and environmental parameters. The causes underlying substrate specificity patterns have been examined for relatively few bryophyte species and for no rare moss species.

Many authors have suggested that substrate specificity patterns in mosses result from physiological limitations, i.e. direct effects of substrate chemistry on survivorship during establishment (e.g., Brown 1982, Robinson *et al.* 1989, Bates & Farmer 1990, Bates 1992, Bates & Bakken 1998). Other studies have proposed that substrate physical characters and disturbance regime may indirectly determine substrate specificity patterns on logs and stumps by affecting the ability of mosses to adhere to substrates (Söderström 1988, Kimmerer 1993, McAlister 1995). Physical constraints on establishment are important on substrates such as logs, stumps, tree trunks and rock faces which experience frequent disturbance and/or which have vertical surfaces where it is difficult for the propagules to adhere.

For instance, Söderström (1988) found that log decay stage and texture related closely to species successional sequences and proposed that this correlation resulted from differential abilities of bryophyte species' propagules to adhere to the wood surface. Kimmerer & Young (1995) also emphasize the importance of a mechanism for propagule attachment to wood by demonstrating that slug slime increased adherence of *Dicranum flagellare* propagules. They reason that any mechanism that increases propagule attachment to the substrate would also increase the chances of propagule establishment.

Didymodon johansenii (R.S. Williams) H.A. Crum is a rare moss species that has been reported as epixylic within its Canadian Rocky Mountain distribution (Crum 1969). Here the species forms small, dense cushions mainly on logs, stumps and tree bases in montane floodplains exposed to aeolian and fluvial deposition of fine silt from mountain glaciers. *Didymodon johansenii* is not a true epixylic species (*sensu* Söderström 1988) as it is not restricted to logs and stumps throughout its range. In the Arctic, *D. johansenii* grows on calcareous soil in the cracks of boulders (Kuc 1973, Steere 1978, Zander 1998). Similarly, in the European Alps the species has been collected growing on small ledges and in cracks of basic rocks with a shallow layer of silt in exposed sites (Pilous 1995, Kučera pers. comm.). While fine silt is strongly correlated with its occurrence on these substrates, the moss does not seem to be physiologically limited by silt during short-term establishment as it can grow equally well on wood covered with acidic, highly organic soil (Cleavitt 2001). However, the silt may serve an important function in attaching propagules to the substrate. This study seeks to clarify the process underlying *D. johansenii*'s observed habitat limitation in Alberta.

In constructing hypotheses about the factors limiting the distribution of a species a useful starting point is to investigate which habitat characters are closely associated with a high probability of species occurrence. The concept of 'suitable habitat' has been used in several studies that focused on epixylic species (Söderström 1988, Hedenäs *et al.* 1989, Söderström 1993). For example, Söderström (1988) related the occurrence and abundance of bryophyte and lichen species to nine log characteristics including maximum log diameter, maximum height of log from the ground, hardness/softness of the log, percent bark cover, wood texture and wood decay stage.

After suitable habitat has been defined for a species, then the relevance of individual variables included in the final habitat model may be tested by gauging the performance of the species in suitable versus unsuitable habitats. Habitat suitability may vary depending on the stage of a plant's life, and for bryophytes there is increasing evidence that species' distributions at many scales reflect restrictions during establishment (Alpert 1988, Li & Vitt 1994, 1995, Kimmerer & Young 1996, see also review by Slack 1997). Therefore, for mosses, regeneration experiments are the most powerful method of testing the importance of habitat factors in limiting species' distribution. In particular, most studies of the bryophyte regeneration niche (*sensu* Grubb 1977) have used gametophyte fragments (e.g., Forman 1964, Rincon 1990, Li & Vitt 1994, 1995, McAlister 1995, Kimmerer & Young 1996), since establishment from spores in the field is difficult to observe and may be infrequent (Miles & Longton 1990, Longton 1994).

Asexual reproduction is likely very important for *D. johansenii* as establishment from spores in the field was not observed for *D. johansenii* during four growing seasons and *D. johansenii* is only known to produce sporophytes in Alberta populations (Crum 1969, Kuc 1973, Steere 1978, Pilous 1995). In addition, sporophyte abortion within Alberta populations may be common as sporophyte production in the field ceased after seta elongation (i.e., early calyptra intact stage of Greene (1960)) in the majority of populations in the study area in both 1999 and 2000 (Cleavitt, pers. obs.). These sporophyte abortion events may have been triggered by abnormally cold summer temperatures since plants aborted after June snowfall events and plants collected in May of both years successfully completed sporophyte development in a 15°C growth chamber. The abortion of sporophytes from unseasonably cold temperatures has also been reported for *Buxbaumia aphylla* in Newfoundland (Hancock & Brassard 1974). It is unknown whether asexual reproduction is also sensitive to environmental conditions.

The importance of physical and environmental habitat parameters to the occurrence and regeneration of the rare moss species, *D. johansenii*, in Alberta were explored to answer the following questions. 1. Do intrinsic log substrate characteristics differ for the logs where *D. johansenii* does and does not occur, i.e., are some logs more suitable and are some log characteristics more important in predicting *D. johansenii* presence? 2. Do environmental parameters (i.e., light, temperature and moisture) differ between the logs defined as 'suitable' and 'unsuitable' for *D. johansenii*? 3. Does presence of silt significantly increase establishment of *D. johansenii*? 4. If there are two sets of plots one where silt is added and one where it is taken away on both suitable and unsuitable logs, then will *D. johansenii* establish and grow significantly better on logs defined as suitable? 5. Is asexual propagule establishment related to log environment?

METHODS

Species taxonomy & recognition.

Didymodon johansenii is in the section Didymodon within the genus and appears most closely allied with members of the *D. rigidulus* complex (Zander 1998). It is most likely to be confused with varieties of *D. rigidulus* and with *D. anserinocapitatus* (Zander & Weber 1997, Zander 1998, Otnyukova & Zander 1998). The most distinguishing features of *D. johansenii* are its swollen leaf tips that are deciduous, small stem size (0.3 – 0.5 cm), and its habit in dense, dark brown cushions (Fig. 4.1a). It shares swollen deciduous leaf tips in common with *D. anserinocapitatus* from which it can be differentiated by larger upper laminal cells, only one layer of guide cells, a weaker costa, and a more compact, less branching habit (Zander & Weber 1997, Zander 1998, Otnyukova & Zander 1998, Cleavitt, pers. obs.). Species names follow Zander (1998) for the genus *Didymodon*, Anderson, Crum and Buck (1990) for other moss species, and Moss (1983) for vascular plants.

Log characterization

All logs and stumps within a restricted random 10.5 m x 21 m area were mapped and characterized at each of three sites where *D. johansenii* occurs along the Snake Indian River in the montane region of Jasper National Park, Alberta (sites 1 – 3; Fig. 4.2). In 1997, logs at site 1 (53°09'10"N, 118°00'77"W) and in 1998 logs at sites 2 (53°09'08"N, 118°00'95"W) and 3 (53°08'78"N, 118°00'56"W) were mapped. For each log or stump, eight characters were recorded: presence/absence of *D. johansenii*, maximum log diameter, maximum height (from underside of the log to ground), percent slope of log, bryophyte species present, species of the log (*Picea glauca*, *Populus balsamifera*, *Salix* sp.), decay stage and the presence/absence of a silt layer. Decay stage was scored on a scale from 0 to 4 (simplified from Söderström 1988): 0 = undecayed with bark intact, 1 = bark falling off, wood still hard, 2 = bark off, wood penetrable with a

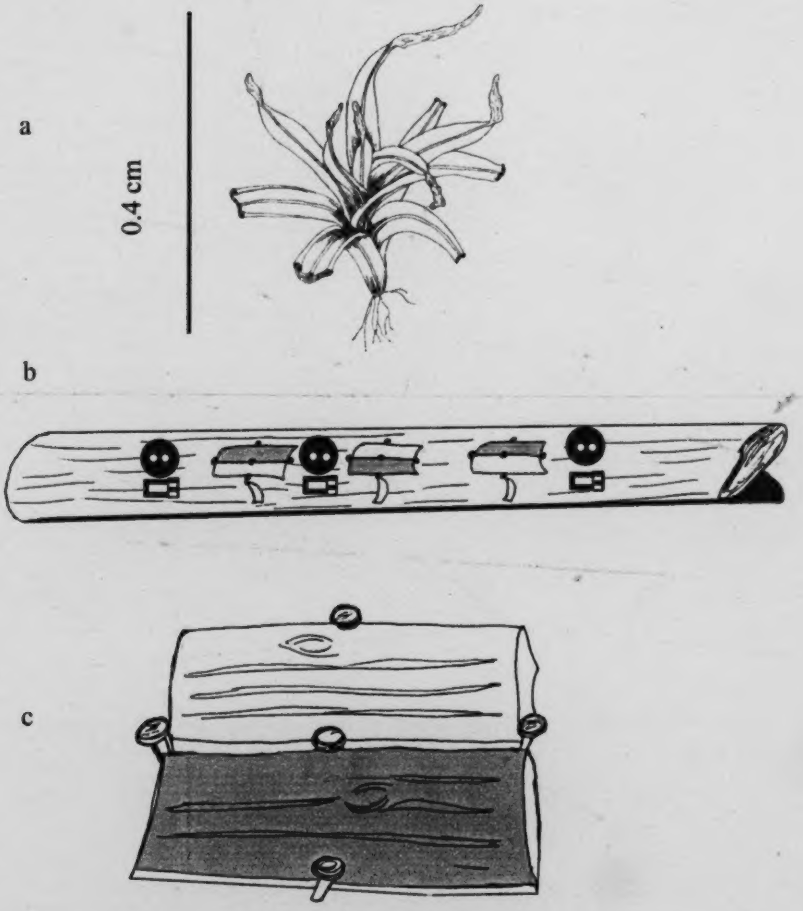

Figure 4.1. Illustrations of the study species and experimental design. a. One stem of *Didymodon johansenii* that displays swollen leaf tips, leaves that have lost their tips, and general leaf habit when hydrated. b. Experimental design for regeneration experiment showing one log with three sets of plots, the grey plots have silt applied. c. Close-up of one pair of plots depicting depressions made by a nail and silt application to only one plot per pair.

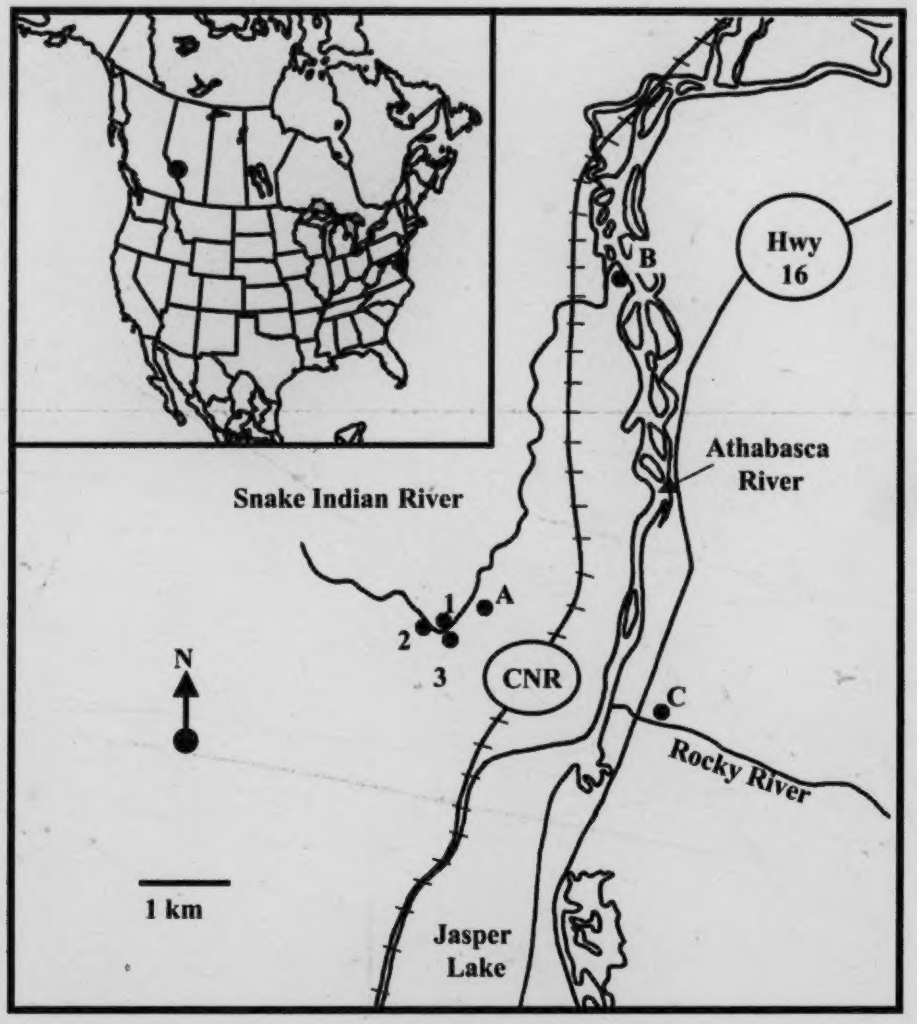
Hwy
16
B
Athabasca
River
Snake Indian River
1
A
2
3
N
CNR
C
Rocky River
1 km
Jasper
Lake

Figure 4.2. Map of Alberta, Canada showing the location of Jasper National Park (gray shaded area) with an enlargement of Devona Flats region, the study area. Sites 1 – 3 along the Snake Indian River were used for log mapping and characterization. Log environmental measurements and gametophyte fragment regeneration experiments were located at sites A – C.

field knife, 3 wood easily penetrable with a field knife, wood with many cracks and beginning to lose its form, 4 = knife able to be inserted to its entire length without effort, log outline greatly distorted. Silt was recorded as present when silt came off onto fingers rubbed over the log surface and/or silt was visible in cracks and knot holes on the log.

From the three sites, a total of 258 logs and stumps were characterized, of which 243 could be identified to tree species. The remaining six log variables with data for all 258 logs were analyzed by logistic regression with *D. johansenii* presence/absence determining variables that significantly contribute to the model of *D. johansenii* occurrence (SPSS 1999, MathSoft 1999). Each log variable was checked for a linear relationship with the logit. Univariate logistic regression models were then run and variable contribution to the model was assessed by both the Wald statistic and their effect on log likelihood of the model (Hosmer & Lemeshow 1989). The variable 'percent slope' was removed from the model because of non-significance. Wald statistics and ratios of estimated coefficient (Coeff) to its standard error (SE) were examined for the five log variables included in the forward-stepwise, multivariate logistic regression model. If the Coeff/SE ratio was less than 0.25, then the variable was removed from the model (Hosmer & Lemeshow 1989). By these criteria, height and maximum diameter were removed from the model. When interaction terms were included in the full final model they did not significantly decrease the deviance of the model compared to a model containing only main effects and their Wald statistics were also non-significant. Model fit was checked by comparing the model deviance to the chi-square distribution with degrees of freedom equal to the number of samples minus the number of parameters included in the model (Hosmer & Lemeshow 1989). A working definition of 'suitable' logs was derived from values of the three variables included in the model where the probability of *D. johansenii* occurrence was greater than random, i.e., 50%. While such a definition is somewhat arbitrary, it allows for objective differentiation between 'suitable' and 'unsuitable' logs.

Measurements of log environment.

In order to minimize disturbance to the mapped sites, three new sites were subjectively chosen for *D. johansenii* presence within the Athabasca River watershed in the montane region of Jasper National Park in May 1999 (Fig. 4.2, sites A, B and C). Site A is located along the Snake Indian River (53°09'50"N, 117°59'82"W) downstream from the prior mapping sites (Fig. 4.2). Site B is situated on the Athabasca River near the confluence with the Snake Indian River (53°11'08"N, 117°59'19"W). Site C is along Rocky River about 1 km east of its junction with the Athabasca River (53°08'56"N, 117°58'46"W).

Using the definitions of 'suitable' and 'unsuitable' logs formulated from log characterization, three equally spaced plots were established on the first seven logs of each group encountered at each site (Fig. 4.1b). Every plot contained a sucrose vial for measuring temperature and a photometer for measuring light. Sucrose vials measure exponential mean temperature by the sucrose inversion method (Damman 1975, Jones & Court 1980). When a buffered sucrose solution is used the rate of sucrose conversion depends only on the temperatures to which the solution is exposed. The amount of sucrose that has been converted to glucose and fructose relates to the light rotation angle of the solution. More sucrose conversion is indicated by a greater difference between the rotation angle of the unexposed (constantly frozen) solution and the exposed solution. Therefore, a greater difference in the rotation angles means that a higher exponential mean temperature was experienced by the solution (Damman 1975, Jones & Court 1980). The sucrose vials measure exponential mean temperature rather than geometric mean temperature because sucrose conversion occurs faster at higher temperatures. Rotation angles were measured on a polarimeter (Perkin Elmer 241) on one second integration interval. Sucrose vials remained on the logs from mid-May to mid-September 1999.

Photometers were used to measure cumulative photosynthetically active light received (Friend 1961, Sullivan & Mix 1983, Matlack 1993). The photometers were constructed from a stack of photosensitive diazo blueprint papers (Western Diazo, Blue 5/Reproblue) that were 2 cm by 4.5 cm and 14 sheets high. These stacks were secured between two paper discs 6 cm in diameter made of black poster board. The top disk had two holes made with a standard paper punch in order to allow the sunlight to expose the diazo paper (Fig. 4.1b). The entire apparatus was protected in a Petri plate sealed with Parafilm and duct tape. The total numbers (including fractions) of exposed sheets were used in the analyses. A greater number of sheets exposed signified higher light levels at a given spot. Sheet fractions are important because the overall relationship of the number of sheets exposed to light intensity is exponential. Photometers were replaced every 14 days from mid-May to mid-September 1999.

During three days with mean daily temperatures greater than 15°C in August 1999, water loss over five hours from late morning to early afternoon was quantified at each site as weight lost from saturated sponges placed on the log beside each environmental plot. The sponges were placed directly on the logs and therefore the measure includes differential water loss not only from evaporation but also from ability of the logs to draw water from the sponges. This simple method of comparing log moisture conditions at each site was chosen because the compact nature of a moss cushion resembles a sponge in their water relations.

Potential differences in environmental conditions of the groups of logs defined as suitable and unsuitable were analyzed by ANOVA calculated by Generalized Linear Model (GLM) using type III sums of squares (SAS Institute 1999). Log was a random variable and nested within the suitability by site interaction. Suitability was a fixed factor and site was a random factor.

Regeneration experiment.

The regeneration plots were set up and planted in May 1999 on the same 42 logs with the environmental plots. Regeneration plots were situated between a sucrose vial and photometer with three pairs of plots per log. Pieces of wood approximately 9 cm by 5 cm by 1 cm were sawn and chiseled out of the logs, and all organisms and silt present on the plot were removed by hand. Each piece of wood was cut into two plots and secured back in its original position (Fig. 4.1b). Pre-cutting of the plots from the logs allowed for whole plots to be brought back to the laboratory. Plots were labeled with flagging tape, scored with a nail to create depressions into which the fragments could be planted, and silt was applied to one plot in each pair (Fig. 4.1c). Silt for the silt treatment was taken from Jasper Lake as this is the most likely natural source of silt on the logs. Silt from the lake-bed has similar consistency and pH to the silt on logs where *D. johansenii* grows (both pH 8.0).

The gametophytic fragments of *D. johansenii* were randomly selected from a pool of fragments that had been collected from the six *D. johansenii* sites and mixed together in distilled water. All rhizoids and sprouts were removed from the fragments under the dissecting scope and were counted into glass vials and stored air dry in the dark until planting. Fifteen fragments 0.2 – 0.3 cm in size representing variation in stem size were planted into each plot in mid-May 1999 by pressing the fragments into the log or silt with forceps.

In September, the plots were removed from the logs and placed in separate plastic bags. Plots were examined under a dissecting microscope and all fragments that could be found were scored as either, 1. dead, 2. alive with rhizoids, 3. alive with sprouts, or 4. alive with rhizoids and sprouts. Data for the plots were combined at the level of each log for ANOVA, so that denominator terms would be available to test all hypotheses in the analysis. Pooling at this level seemed preferable to post-hoc pooling of terms, since the hypotheses of the experiment pertain to differences in regeneration at the log level. The numbers of fragments found, the numbers of fragments alive, and the proportions of those sprouting among those that were alive were analyzed by ANOVA with site random, suitability fixed, silt fixed, and log nested within site by suitability interaction. This ANOVA design was run in General Linear Model (GLM) using type III sums of squares (SAS Institute 1999).

The dataset for numbers of fragments sprouting was both unbalanced (because not all plots had fragments that sprouted) and non-normally distributed. Sprouts had a skewed, Poisson distribution more typical of count data and were analyzed by log linear GLM (MathSoft 1999). The saturated model and subsets of the full model were run to check for significant interaction terms. Only main effects were significant in the model as there were no significant interaction terms. Based on estimated coefficient/standard error ratios (Hosmer & Lemeshow 1989), all variables contributed significantly to the model. The proportions of fragments sprouting were included as an offset in the main effects model to test whether this improved the model fit (i.e., is the number sprouting constant in relation to the number of fragments alive). Residual deviance for models with and without outliers were compared as analysis of residuals suggested that the removal of three outliers from the data set might improve model fit. The possibility of a direct relationship between environmental variables and regeneration was also explored by two-tailed non-parametric correlation (Spearman's rho) between the numbers of fragments alive and sprouting and log temperature, light, and water loss (SPSS 1999).

RESULTS

Didymodon johansenii was present on 120 out of 258 logs. Differences in log characteristics between logs with and without *D. johansenii* are shown in Figure 4.3. Only slope of the log and log species (not shown) did not differ between these two log groups (Mann Whitney U, p = 0.691 and G-test, p = 0.534, respectively). Logs with *D. johansenii* were closer to the ground, of larger diameter and in later decay stages with greater frequency of a silt layer and higher bryophyte species richness (Fig. 4.3).

The final logistic regression model included the number of other bryophyte species, silt layer presence, and decay stage (Table 4.1). The number of other bryophyte species on the log was the best single explanatory variable for modeling *D. johansenii* occurrence and the probability of *D. johansenii* occurrence increased with species richness (Table 4.1). Silt layer and decay stage both contributed similarly to model deviance reduction and were both positively related the probability of *D. johansenii* occurrence (Table 4.1). 'Suitable' habitat for *D. johansenii* in Jasper National Park, Alberta consists of logs with 4 or more other bryophyte species present, with a silt layer, and in decay stage 3 or 4. By this definition, *D. johansenii* occurred on 78% of the suitable logs.

There were no significant differences between sites for water loss and temperature; however, there was a significant site by log suitability interaction for light (Table 4.2, Fig. 4.4). This interaction resulted from higher light on suitable logs at site B in contrast to lower light levels on suitable logs at sites A and C (Fig. 4.4a). Site A had the largest difference in light levels between suitable and unsuitable logs (Fig. 4.4a). Sponges on suitable logs lost significantly less water than sponges on unsuitable logs at all sites (Table 4.2, Fig. 4.4b). Temperature was not significantly different between log type (Table 4.2), although at site A, temperatures were much lower on suitable versus

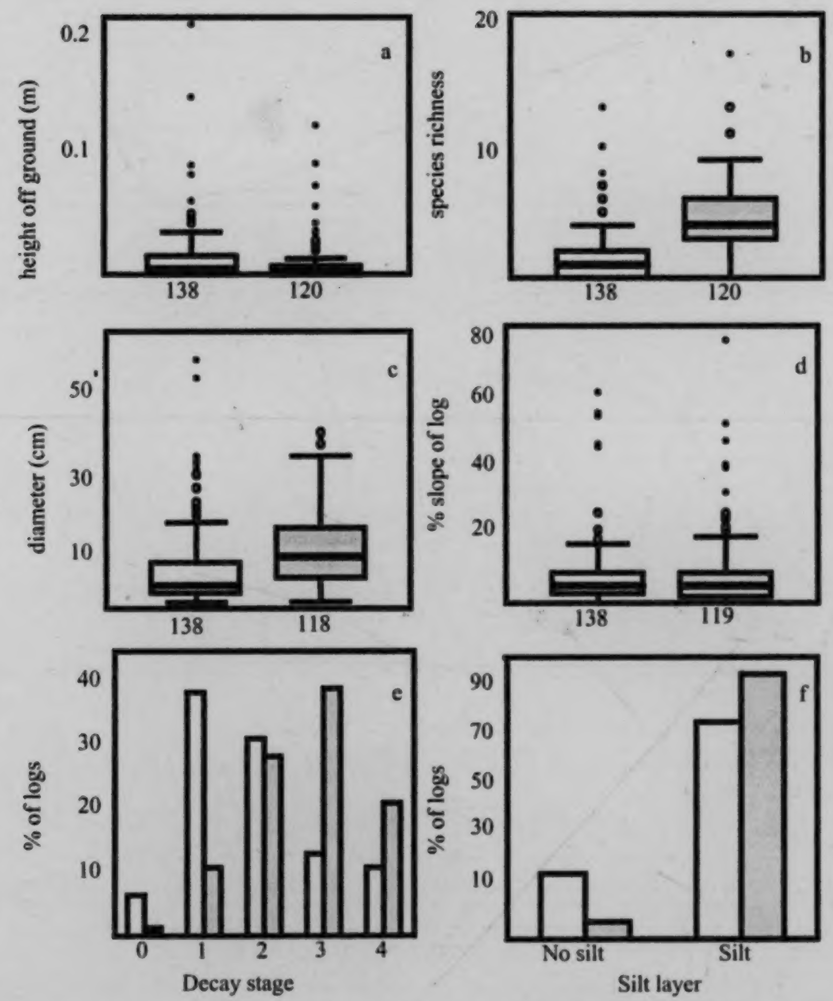

Figure 4.3. Comparison of log characteristics scored for 258 logs at sites 1 – 3 for logs without (unshaded) and with (shaded) *D. johansenii*: a. Maximum log height from the ground, b. Species richness, c. Maximum log diameter, d. Percent slope of logs, e. Decay stage distribution, and e. Silt layer presence/absence. For the box plots, the heavy horizontal bar represents the median. The box represents the range of 50% of the data while the vertical bars show the interquartile range. Circles and asterisks signify data outliers and extreme values. The number of logs included in each category is given below the x-axis.

Table 4.1. Logistic regression model relating log variables to *D. johansenii* occurrence. a) Model building: percent change in deviance attributable to log variables. Variable degrees of freedom are given beneath the variable abbreviation in parentheses. Significance of actual change in deviance signified by: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. All relationships found to *D. johansenii* occurrence were positive, e.g., the probability of *D. johansenii* occurrence increased with increasing species richness. Non significant variables were removed from the model. The final model: Intercept + othspp + silt + decay had a deviance of 254.657 on 253 degrees of freedom ($r^2 = 0.429$) and classified 75.74% correctly for *D. johansenii* absence, 77.78% for presence, and 76.68% overall.

Model	df	Other species (1)	Silt presence (1)	Decay stage (4)	Max diameter (1)	Height (1)	Percent slope (1)
Intercept +		24.69***	13.50***	15.97***	5.38***	1.63*	0.14
Intercept + othspp +			6.81***	7.51***	0.45	0.16	
Intercept + othspp + silt +				6.26**			

b) Model variable deviance reduction, coefficients and associated standard errors.

	Model deviance reduction (step)	Estimated coefficient	Standard error of coefficient
Full model	98.73		
Best model	96.61		
othspp	67.66	0.367	0.075
silt	15.86	-1.406	0.475
decay	13.09		
decay (1)		-1.518	1.478
decay (2)		-0.363	0.562
decay (3)		0.524	0.498
decay (4)		1.027	0.489
constant		-1.327	0.538

Table 4.2. Results of ANOVA for three environmental variables measured at three sites with seven logs classified as suitable and seven as unsuitable for *D. johansenii* habitat. F-values and their significance are shown. Significance values: ns = not significant at p=0.05, * p<0.05, ** p<0.01, *** p<0.001.

	Temperature	Light	Water loss
Site	0.48^{ns}	0.62^{ns}	16.00^{ns}
Suitun	3.72^{ns}	1.43^{ns}	25.69*
Site x suitun	2.87^{ns}	7.31**	0.17^{ns}
Log (site x suitun)	4.55***	8.63***	3.29***

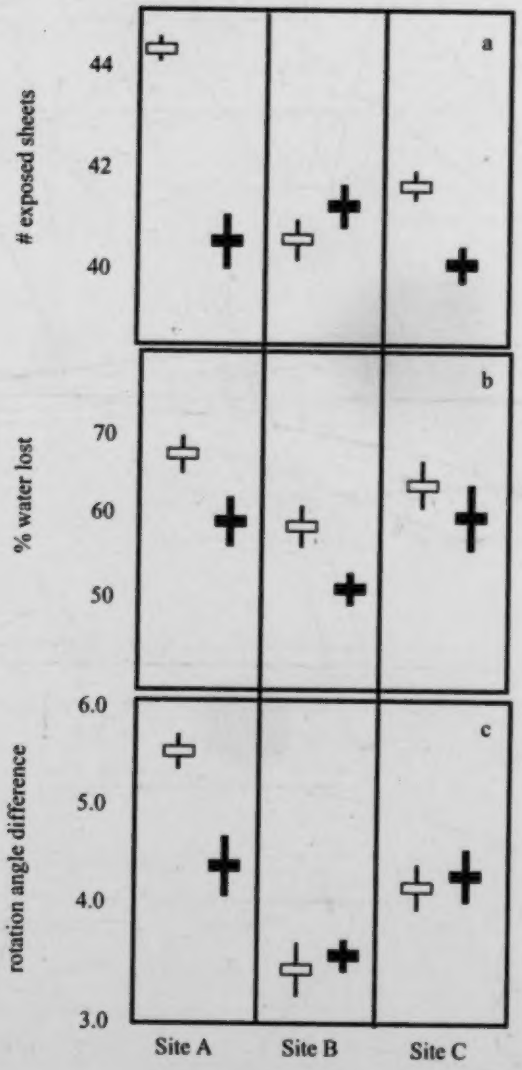

Figure 4.4. Summary of mean environmental parameters measured at sites A – C on seven unsuitable (white) and suitable (black) logs per site. Error bars represent standard error of the mean. Parameters are the means from three replicates on each log (for seven logs, N = 21). a. Cumulative photosynthetically active light received from 20 May – 16 September 1999. b. Percent water lost from saturated sponges over five hours in August 1999. c. Mean biological temperature from 20 May – 16 September 1999.

unsuitable logs (Fig. 4.4c). Temperature, light and water loss differed significantly between logs regardless of log type (Table 4.2).

Overall, the proportion of planted fragments that were found after four months was low (15.53 ± 20.95%). However, 94.15% of fragments found were alive and regenerating. The number of fragments found and alive was significantly higher on silt plots (Tables 4.3 & 4.4, Fig. 4.5). When all species were removed and silt presence was manipulated, log suitability (mainly a proxy for decay stage) did not explain differences in adherence and survivorship of fragments (Table 4.3, Fig. 4.5). The number of fragments sprouting was best predicted by the number of fragments alive; however, silt presence also explained a significant portion of model deviance reduction (Table 4.4). The effect of silt on sprouting was consistent across sites and log suitability, i.e., there were no significant interaction terms in the model (Fig. 4.6, Table 4.4). The significant deviance reduction gained by including the offset of proportion of fragments sprouting out of those alive indicates that sprouting increases in proportion to the number of fragments alive. Environmental variables were not correlated to fragment survivorship and growth (Spearman's rho, 2-tailed, all $p > 0.05$).

DISCUSSION

Log suitability.

Although logs with and without *D. johansenii* differed significantly in maximum log diameter, maximum height from the ground, decay stage, bryophyte species richness and silt layer presence (Fig. 4.3), only bryophyte species richness, silt layer presence and decay stage significantly contributed to predicting *D. johansenii* presence (Table 4.1). *Didymodon johansenii* is more likely to be present on logs with higher species richness, a silt layer and in later decay stages. The lack of importance of the tree species for logs differs from the findings of Andersson and Hytteborn (1991) for epixylic bryophytes in Sweden. However, the presence of a silt layer between the log and *D. johansenii* may explain the lack of importance of log species in this case, since the moss is not in direct contact with the log. The specificity of bryophytes to log species probably varies from region to region and from site to site as it does for epiphytes (Palmer 1986). Palmer

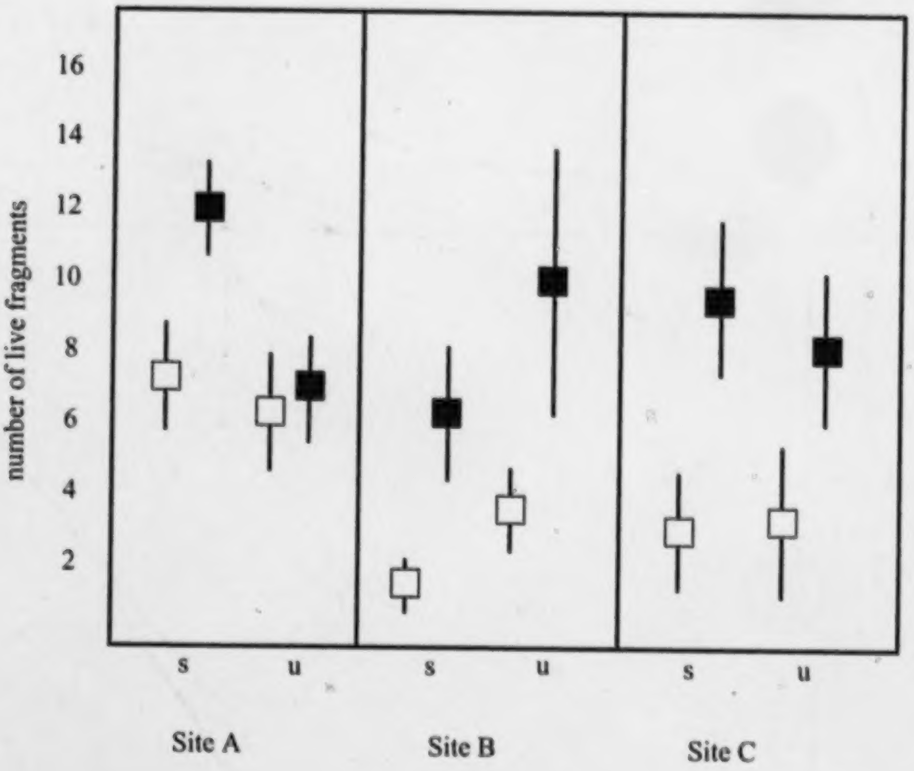

Figure 4.5. Comparison of *Didymodon johansenii* gametophyte fragment survivorship at sites A, B and C on seven suitable (s) and seven unsuitable (u) logs per site, on no silt (white) and silt (black) plots. Error bars represent a standard error above and below the mean. Site and suitability are abbreviated on the x-axis.

Table 4.3. ANOVA of found and live fragments at three sites on suitable and unsuitable logs and plots with and without silt (model d.f. = 83). Significance values: ns = not significant at p=0.05, * p<0.05, ** p<0.01, *** p<0.001.

Source	d.f	MS found	MS live	Error MS	F found	F live
1) site	2	43.73	60.73	(8)	1.56^{ns}	2.15^{ns}
2) suitun	1	0.107	0.964	(5)	0.00^{ns}	0.02^{ns}
3) site x suitun	2	83.82	62.18	(8)	2.99^{ns}	2.20^{ns}
4) silt	1	540.1	462.0	(9)	19.56***	18.28***
5) site x silt	2	28.32	20.51	(9)	1.03^{ns}	0.81^{ns}
6) suitun x silt	1	7.440	10.01	(7)	0.26^{ns}	0.73^{ns}
7) site x suitun x silt	2	28.23	13.73	(9)	1.02^{ns}	0.54^{ns}
8) log (site x suitun)	36	28.04	28.23			
9) silt x log (site x suitun)	36	27.61	25.28			

Table 4.4. Log linear analysis of number of sprouting fragments. Final model: Sprout = Site + Suitability + Silt + Live + offset (sprouts/live). The null model deviance was 98.394 on 70 degrees of freedom and the final model residual deviance was 43.281 on 66 degrees of freedom. For variable deviance explained an * indicates significance at $\alpha = 0.05$ on χ^2 distribution with 1 degree of freedom.

	Estimated Coefficient	Standard Error	Coeff/SE	Deviance explained
Constant	-1.102	0.358	-3.08	
Site	-0.112	0.124	-0.96	2.144
Suitability	0.370	0.209	1.77	2.984
Silt	0.272	0.254	1.07	9.919*
Live	0.111	0.017	6.39	40.06*

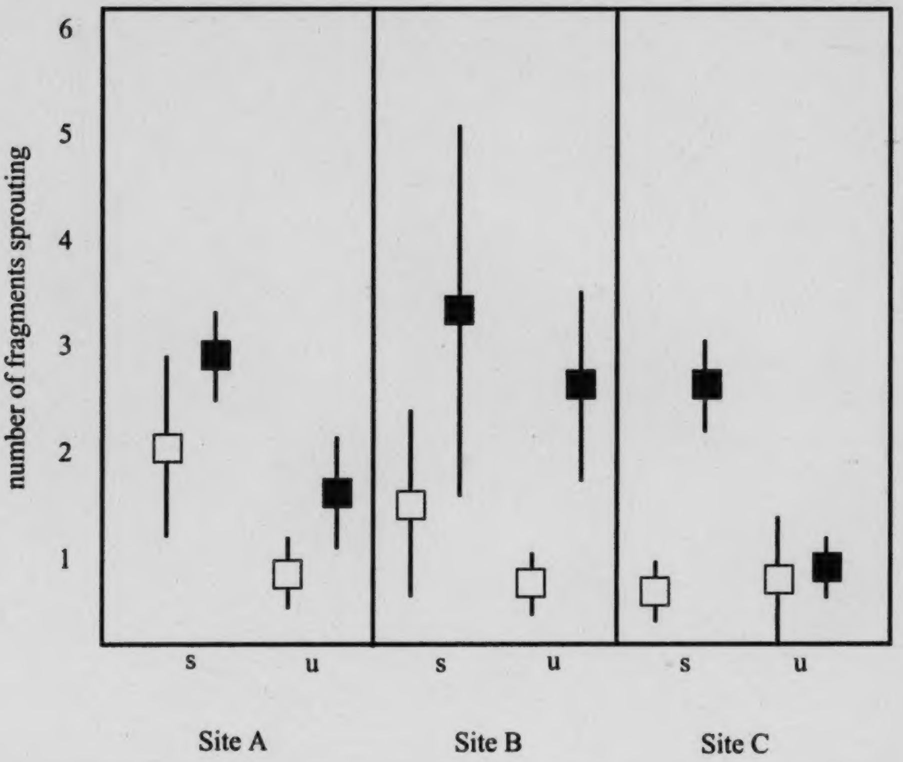

Figure 4.6. Summary of *Didymodon johansenii* gametophyte fragment sprouting at sites A, B and C on seven suitable (s) and seven unsuitable (u) logs per site, on no silt (white) and silt (black) plots. Error bars represent a standard error above and below the mean. Site and suitability are abbreviated on the x-axis.

(1986) compared host tree specificity of epiphytes in North Carolina between sites and with findings of Culberson (1955) in Wisconsin and Studlar (1982) in Virginia. He found that epiphyte species segregate along the same complex pH-moisture gradients between sites and geographical regions regardless of host tree species present at the sites (Palmer 1986).

The definition of suitable habitat for *D. johansenii* serves not as an absolute description of the only habitat where the moss can grow, but rather as an objective means of distinguishing habitats where it is more likely to grow in Alberta. Species richness, silt layer presence, and log decay stage were identified as habitat characteristics meriting experimentation to clarify the habitat restrictions of *D. johansenii*. Of these, the presence of a silt layer was easiest to manipulate experimentally. In addition, decay stage and bryophyte species richness have a more ambiguous relationship to the occurrence of this species since *D. johansenii* most often occurs on the least decayed parts of older logs, especially on protruding branches without other species present. Hence although later decay stages and the number of other bryophyte species present are significantly correlated to *D. johansenii* occurrence, this correlation probably resulted from a shared positive relationship of all three variables to time available for deposition/colonization rather than a direct relationship to each other. Species richness and log decay stage are more complex variables to evaluate because both are correlated to many other factors such as log age and history, and are often correlated to one another (Söderström 1988, Andersson & Hytteborn 1991).

Since all other species were removed from the regeneration plots, the importance of other species to *D. johansenii* establishment was not tested in this study, and the analysis of suitability effects is best interpreted as a preliminary test only of the importance of decay stage. The full complexity of decay stage such as variation in log texture and moisture holding capacity (Söderström 1988, Andersson & Hytteborn 1991) and the effects of bryophyte species richness on *D. johansenii* have not been tested. However, the lack of log suitability effects once silt presence has been controlled for suggests that predictive value of the decay stage was not based on a direct species-substrate interaction.

Suitable logs did not differ greatly in terms of environmental parameters from unsuitable logs; however, water loss was lower on suitable logs and there was variability between the environments of individual logs (Table 4.2). The site by log suitability interaction for light resulted from the greater exposure of the suitable logs at site B (Fig. 4.4a). At site B, 'suitable' logs were all low-lying willows on the more open riverbank edges of the site. The lack of clear environmental differences between suitable and unsuitable logs suggests either that log suitability criteria and/or environmental measurements were not accurate enough or that the measured environmental parameters are not important for determining the presence of *D. johansenii.* The absence of fragment response to differences in these log environmental factors favors the latter hypothesis. This conclusion agrees with that of Heegaard and Hangelbroek (1999), who found inherent substrate factors to be more significant than environmental factors for explaining the distribution of the epiphyte, *Ulota crispa,* in Norway.

Didymodon johansenii establishment.

The presence of silt increased the numbers of gametophyte fragments found, the numbers alive and the numbers sprouting. Its influence on fragment survival was through increased fragment adherence as the number of fragments surviving out of those found did not differ significantly between plots with and without silt. This result concurs with Cleavitt (2001), where *D. johansenii* was able to regenerate on a substrate that was chemically the opposite of its native substrate, i.e., the moss can establish on acid, high organic content soil as well as on calcareous, mineral silt. Despite the absence of a strong physiological limitation to silt, the importance of silt in *D. johansenii* ecology is apparent throughout its range (Kučera pers. comm., Pilous 1995). Silt has many physical properties that may increase establishment. For instance, silt provides a much easier medium to grow through than wood or rock and calcareous silt hardens upon drying thereby cementing fragments to the substrate. Regenerating fragments in silt often had more extensive rhizoid growth than fragments on non-silt plots. The correlation between the number of fragments sprouting and silt suggests that fragments on silt may also have higher growth rates. Moss water relations appear more closely related to substrate type than to ambient humidity (Hernández-Garcia *et al.* 1999). The fine particle size of the silt, by holding water through capillary action, may slow down the rate of moss drying, and thereby allow relatively longer metabolically active time periods while perhaps also lessening the stress of desiccation.

Conclusion.

Within Alberta, the restriction of *D. johansenii* to the mountains relates to its requirement for fine, calcareous silt of glacial origin, which significantly increases the probability of establishment and may also influence subsequent propagule growth rates. This study joins with Kimmerer and Young (1996) in demonstrating the importance of the regeneration niche for log and stump dwelling moss species and confirms the intimate relationship of propagule adherence to propagule establishment on logs hypothesized by Söderström (1988), McAlister (1995), and Kimmerer and Young (1996). The demonstration of physically based substrate limitation advances our understanding of the ecology of this rare moss, but does not preclude the possible role of biotic interactions in further determining *D. johansenii* occurrence. Studies exploring biotic interactions such as the competitive ability of *D. johansenii* would afford a more complete picture of factors limiting this species, and further clarify the relative importance of its physical limitation to specific substrates.

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Chapter 5: Physiological tolerance of six moss species as colonies and fragments measured by exposure to short- and long-term stress

Investigations of species local distribution limits require determination of the correspondence between habitat environmental conditions and the physiological tolerance of a species (e.g., Walters & Field 1987, Dale & Causton 1992, Robson & Maze 1995, Sultan *et al.* 1998). Physiological tolerance of adult plants can correspond to habitat environmental conditions (e.g., van Auken & Bush 1997, Sultan *et al.* 1998), but not always (e.g., Walters & Field 1987, Baskauf & Eickmeier 1994, Greulich *et al.* 2000). The ability of species to respond to environmental stresses is increasingly recognized to influence species local distributions (Baruch & Smith 1979, Dale & Causton 1992a, b, c d, Geber & Dawson 1997, Sultan *et al.* 1998, Baruch, Pattison & Goldstein 2000, Valladares *et al.* 2000, Novoplansky & Goldberg 2001). Lack of correlation between physiological tolerance of adult plants and environmental conditions can be attributed to species interactions (e.g., competition, facilitation) or physiological limitations encountered by the species earlier in their life cycle (e.g., dispersal and recruitment) (Hutchinson 1957, Grubb 1977). Dispersal to a site, a prerequisite for site occupation, may require stress tolerance in the plant propagule stage of conditions dissimilar to those where the species in generally found. Differences in propagule viability can explain differences in local distribution patterns of some species (Rand 2000). In this paper, I compare the degree of environmental stress (e.g., desiccation and high light intensities) in adult plant habitats to the ability of six moss species with different distribution patterns to tolerate these stresses as adult colonies and as vegetative propagules. Particular emphasis is placed on stress responses of vegetative propagules and their potential role in determining colonization potential for three rare-common species pairs.

Dispersal ability relies on the quantity and type of propagules available, propagule viability, and relative efficiency of propagules in being carried by dispersal vectors such as wind and water (Silvertown 1987, Söderström 1989). Propagule viability after transport or simulation of transport has been used as a first approximation of the dispersal ability of bryophyte spores and gametophyte fragments (van Zanten & Pócs 1981, van

Zanten & Gradstein 1988, Dalen & Söderström 1999), and less attention has been given to propagule availability and dispersal vectors. The quantity and type of propagules produced depends on relative allocation to sexual versus asexual reproduction. Moss species vary in their reliance on asexual reproduction both within (Kimmerer 1994) and between species (Longton & Schuster 1983, Newton & Mishler 1994). Asexual reproduction, especially through gametophyte fragments, is the sole or main means of reproduction for many species (Longton & Schuster 1983, Longton 1994, 1997), and these species are more successful at establishing from fragments than species that allocate more energy to spore production (Miles & Longton 1990, Longton 1997). There is evidence of a trade-off between investment in sexual versus asexual reproduction in bryophytes and vascular plants (Kimmerer 1991, 1994, Laaka-Lindberg 2001, Ronsheim & Bever 2000).

Although, most bryophytes seem capable of reproducing from gametophyte fragments, not all species have the highest regeneration through this mode of reproduction. For instance, gametophyte fragments had lower viability than spores in five moss species with frequent sporophyte production (Dalen & Söderström 1999). In contrast, *in situ* viability of gametophyte fragments has been found to be greater than spore viability in propagule bank studies (During 1992, 1997). Asexual and sexual propagules appear to have different roles, with spores being more important for colonist species and gametophyte fragments being more important for long-lived species (During 1992). Spores are physiologically capable of long-distance dispersal (van Zanten & Pócs 1981, van Zanten & Gradstein 1988), but it remains less clear whether gametophyte fragments or other asexual propagules also have this physiological capability. This capability is explored here for long-term transport of gametophyte fragments in air and water. Dispersal ability is described here in terms of observed differences in species allocation to sexual reproduction, success of asexual reproduction via vegetative fragments, and vegetative propagule viability as affected by both length and conditions of storage.

Despite the potentially central role of gametophyte fragments in bryophyte ecology, research on gametophyte fragment physiology has not been undertaken. When compared to other land plants in terms of physiology, bryophytes are typically shadeadapted and have similar osmotic potentials to one another, low chlorophyll *a*/*b* ratios, and relatively low light saturation levels (Proctor 1999). Consequently, optimal conditions for bryophyte physiological activity are quite similar to one another regardless the environment where they occur (Alpert & Oechel 1985, Proctor 1999). However, bryophytes do vary in stress responses such as desiccation tolerance and tolerance of high light levels, and it is these differences that have been particularly central to explaining differences in habitat occupation (e.g., Bushby *et al.* 1978, Seel *et al.* 1992, Csintalan *et al.* 1999). Evidence from many bryophyte desiccation studies indicates that species from xeric habitats are more desiccation tolerant than species from mesic habitats (Brown & Buck 1979, Seel *et al* 1992, Oliver *et al.* 1993, Deltoro *et al.* 1998, Csintalan *et al.* 1999, Robinson *et al.* 2000). Whether the stress tolerance of vegetative propagules also reflects source habitat conditions is unknown.

Propagule stress tolerance in vascular plants has been shown to correspond to stresses apparent in plant habitats (Khurana & Singh 2001, Koval 2000). Overall, long term viability of terrestrial plant propagules largely depends on their ability to withstand prolonged desiccation (Bewley 1995, Khurana & Singh 2001). This important aspect of seed viability, desiccation tolerance, is analogous to the vegetative desiccation tolerance of moss gametophyte tissues (Bewley 1995). It is, however, unclear whether vegetative desiccation tolerance in mosses is reflected in vegetative propagule viability after exposure to water stress. Correspondence between propagule viability and parent plant physiology could be strong if short-term and long-term stress responses are correlated to one another. In addition, different types of stress response may be correlated. For example, resistance to photosystem damage from high light levels has been correlated with desiccation tolerance in mosses (Seel *et al.* 1992). Such linkages, if also expressed through differential propagule viability, may be important in understanding dispersal limitations of species lacking certain stress responses.

In contrast, the relationship between source site environmental conditions and tolerance limits of propagules may be decoupled in situations where dispersal between habitats requires propagules to survive environmental conditions very different from those experienced by stationary colonies. Depending on the mode of dispersal, transport may involve stresses such as desiccation, exposure to high light intensities and submersion in water. Even in habitats presenting relatively continuous environmental conditions, propagules must survive exposure to the surrounding environment without the benefit of micro-environment modification associated with adult plant architecture (Proctor 2001). These potential decoupling factors may be especially pertinent for small plants such as mosses that perceive habitat differences at a fine scale (Birks *et al.* 1998) and that tend to occupy discontinuous habitats (Söderström 1995). The ability of bryophyte propagules to tolerate stresses during movement between patches must influence the maintenance and spread of local populations and resulting species distribution patterns (Hanski 1982, Söderström 1989, Herben, Rydin & Söderström 1991, Marino 1991).

A classic delineation in species distribution patterns is that between rare and common species. Many theories have arisen to account for differences in rare and common species distributions (e.g., reviews by Fiedler 1986, Rabinowitz 1981, Fiedler & Ahouse 1992, Kunin & Gaston 1997), including theories concerning differences in the physiology and dispersal ability of rare and common species (Hanski 1991, Holt *et al.* 1997). Comparative studies of rare-common species pairs remain the most robust means of testing the generality of such theories (Rorison *et al.* 1987, Grime *et al.* 1988, Baskin *et al.* 1997). In this comparative study of three rare and three common moss species the following questions are addressed: 1) Do species vary in the relationship of colony source site environment to species stress tolerance? 2) Do any of the stress responses tend to co-occur within species? 3) Does propagule viability correspond positively with asexual reproduction emphasis for these species? In addition, results are interpreted with respect to rarity theory.

METHODS

Study species and sites.

The six species used in this study differ in geographic range size, local habitat preferences and frequency of sporophyte production. Study species selection criteria are outlined in the methods of Cleavitt (2001). The three species pairs, with the rare species listed first, are *Mielichhoferia macrocarpa* (Hook) Jaeg. and *Bryum pseudotriquetrum*

(Hedw.) G.M.S., *Didymodon johansenii* (Williams) Crum, and *Didymodon rigidulus* Hedw. var. *gracilis* (Schleich.) Zand., and *Mnium arizonicum* Amann and *Mnium spinulosum* Bruch. & Schimp. *Didymodon rigidulus* var. *gracilis* will be referred to as *D. rigidulus* throughout the rest of this paper.

Mielichhoferia macrocarpa and *D. johansenii* are globally rare with widely disjunct distributions (Shaw & Rooks 1994 and Pilous 1995, respectively) while *M. arizonicum* is endemic to North America (Koponen 1972). *Bryum pseudotriquetrum* and *D. rigidulus* are widely distributed in the northern and southern hemispheres (Crum & Anderson 1981 and Zander 1994, respectively) while *M. spinulosum* is restricted to the northern hemisphere (Koponen 1981). *Mielichhoferia macrocarpa* grows in locations that are not flooded but remain constantly wet by seepage during the growing season (pers. obs., Brassard & Hedderson 1983). *Bryum pseudotriquetrum* occurs in many moist habitats such as stream banks, roadside drainage ditches and lake shores that may experience seasonal flooding (pers. obs., Crum & Anderson 1981). *Didymodon johansenii* and *D. rigidulus* are found in xeric sites (Zander 1981, Kučera 2000), although *D. johansenii* typically grows in more protected microsites than *D. rigidulus* (pers. obs., J. Kučera pers. comm.). *Mnium arizonicum* typically occurs at higher elevations than *M. spinulosum* and occurs in both sheltered tree stands and more exposed habitats in the sub-alpine (pers. obs, Koponen 1972). *Mnium spinulosum* is found in boreal coniferous forest in typically mesic, low light conditions (Steere 1978, Crum & Anderson 1981).

Study sites were located in the eastern Front Ranges and Foothills of the Canadian Rocky Mountains, mostly in Whitehorse Creek Wildland Park and Jasper National Park, Alberta, Canada (Fig. 5.1, inset). Sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum* are located largely within the Whitehorse Creek Wildland Park (elevation 1600-2000m) (Fig 5.1). *Mnium spinulosum* sites are located at lower elevations, 1400-1410m, in the Foothills ecoregion on Weldwood of Canada Ltd. property along Cold Creek Road. *Didymodon johansenii* and *D. rigidulus* sites are located at the lowest elevations (1050-1150m) in the montane ecoregion of Jasper National Park (Fig 5.1).

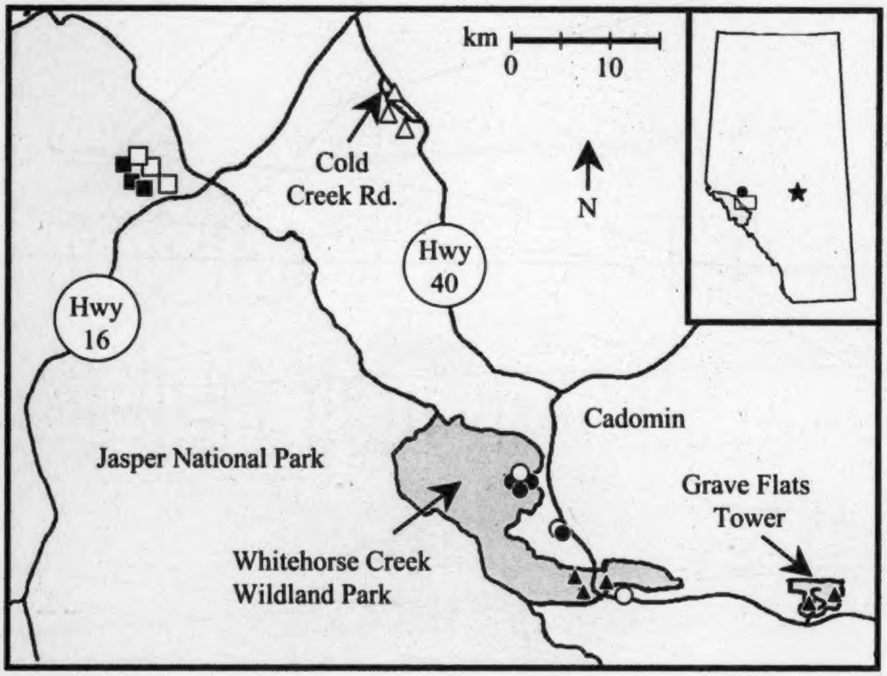
km
0
10
Cold
Creek Rd.
N
Hwy
40
Hwy
16
Cadomin
Jasper National Park
Grave Flats
Tower
Whitehorse Creek
Wildland Park

Figure 5.1. Map of study area showing general location of sites used for the six study species. Some sites are obscured because of close proximity to one another. There are five sites for all six species. Site symbols correspond to species symbols used throughout the figures in this paper: *M. macrocarpa* (●), *B. pseudotriquetrum* (○), *D. johansenii* (■), *D. rigidulus* var. *gracilis* (□), *M. arizonicum* (▲), and *M. spinulosum* (△). Inset map shows the province of Alberta and the position of Jasper National Park (gray) and the area of enlargement (rectangle) within Alberta. The cities of Edmonton (star) and Hinton (dot) are shown for reference.

Characterization of colony environments.

Moisture.—To compare moisture availability and evaporation rates between habitats occupied by the six species, two methods were employed: 1) gain in water content of initially dry sponges throughout a growing season (1998), and 2) loss of water from saturated sponges over a 5-hour period under sunny, summer conditions when evaporation rates were expected at their maximum in each habitat (1999). Sponges for both experiments were made of synthetic plastic and were cut to approximately 3.5cm x 3.0cm x 2.0cm in size.

In 1998, dry sponges placed into moss colonies were monitored by weighing the sponges at the field sites with a pesola scale. There were six sponges at five replicate sites per species and sponges were weighed every ten days from May to September. Sponge water content differences measured in 1998 paralleled differences in moss water contents measured in 1999 (data not shown). This indicates both that the sponges mimic moss water retention and that habitat moisture characteristics were similar between 1998 and 1999. The sum of all water measurements for the season, total net grams of water gained by the sponges at each site, was used in the analysis (n = 5 for each species).

In 1999 at three replicate sites per species, water loss from saturated sponges was measured over five hours on days with mean average daily temperatures above 15°C and clear skies. At each site, there were at least five replicate sponges, although more replicates were used in habitats where moisture and light conditions were more heterogeneous. Water loss sponges were artificially saturated with water and their initial weight (Ohaus Scout portable scale) was recorded. Sponges were placed next to or among moss colonies and re-weighed at 2.5 and 5 hours. Averages of water loss per sponge for each site were used in analysis of the data (n = 3 for each species). Water gain and water loss data were analyzed by one-way ANOVA by species with Tukey HSD post-hoc test.

Light.—Habitat light measurements were taken repeatedly for a period of ten days throughout the 1998 field season using photosensitive Diazo blueprint paper to measure cumulative photosynthetically active light received (Friend 1961, Sullivan & Mix 1983, Matlack 1993). Photometers were composed of a stack of photosensitive diazo blueprint paper (Western Diazo, Blue 5/Reproblue) between two black paper discs. The top disk had two holes made with a standard paper punch in order to allow the sunlight to expose the diazo paper. The entire apparatus was protected in a Petri plate sealed with Para film and duct tape. Light levels were indicated by the number of sheets exposed. The number of sheets exposed included partially exposed sheets at the bottom of the stack. Partially exposed sheets were scored as ¼, ½ or ¾ exposed and inclusion of these sheets is important because the overall relationship of the number of sheets exposed to light intensity is exponential (Friend 1961, Matlack 1993). The mean number of sheets exposed in three photometers per site were recorded repeatedly for a ten day period at each site. Ten-day means for each site were summed for the season to obtain total cumulative photosynthetically active light received at the site. There were five replicate sites for each species and these were the same sites used for 1998 sponge water change measurements. Light data were analysed by one-way ANOVA by species with Tukey post-hoc test. The relationship between habitat mean light levels and mean water loss was examined by Pearson correlation.

Short-term stress responses of colonies and gametophyte fragments.

Short-term stress response was measured on colonies and gametophyte fragments using chlorophyll fluorescence. Colonies are groups of moss stems that have a definable boundary and three-dimensional architecture. In all colony experiments, special effort was made to maintain the colony architecture when plants were placed into the fluorometer leaf clip. In gametophyte fragment experiments, individual stems were placed onto the leaf clip to fill the clip area and colony architecture was completely disassembled.

Chlorophyll fluorescence.—Short-term responses to environmental stress were detected by changes in chlorophyll fluorescence using a pulse amplitude modulation (PAM) fluorometer (Walz, Effeltrich, Germany, model PAM-2000). Chlorophyll-fluorescence measurements allow rapid, non-invasive assessment of physiological state of a plant (Bolhàr-Nordenkampf & Öquist 1993, Seel *et al.* 1992, Csintalan *et al.* 1999.). The basic parameters of fluorescence and derived quantities pertinent to this study are illustrated in Figure 5.2. In this study, dark- and light-adaptation refer to plants that had

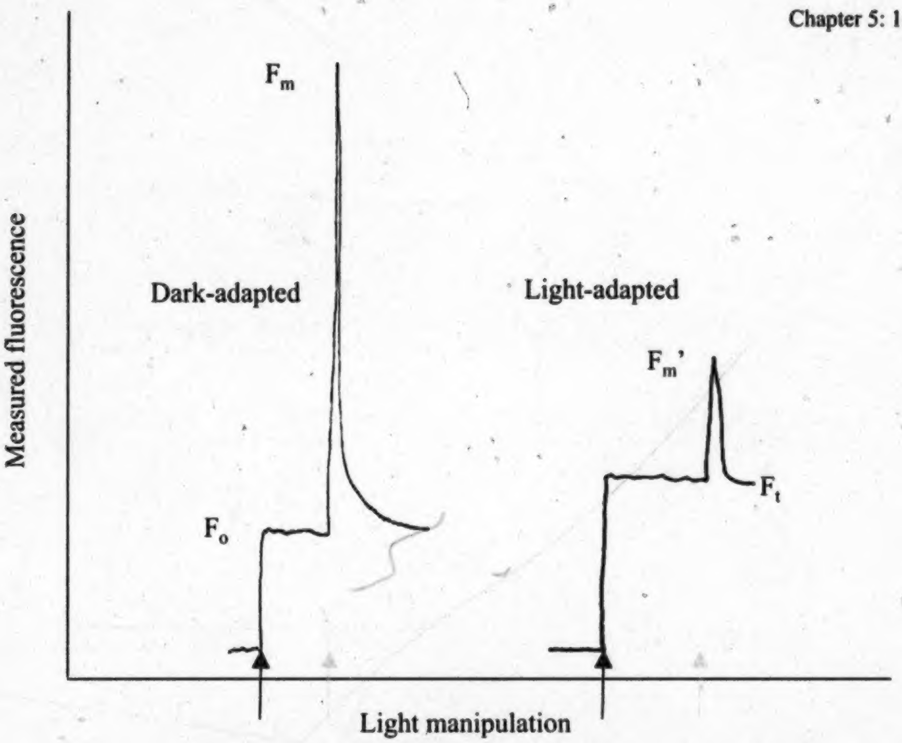

Figure 5.2. Diagram depicting the relationship of fluorometer variables used in this study. F_o is the minimal or basal level of fluorescence emitted when a dark-adapted sample receives light from the modulating beam that is at an intensity too low to activate photosystem II. F_m is the upper or maximal fluorescence emitted by the plant when struck by a saturating flash of light that is bright but too brief to activate photosystem II. The difference between F_m and F_o is called variable fluorescence or F_v. F_v/F_m is the maximum quantum yield of photosystem II. A similar relationship exists for fluorescence measurements taken on light-adapted plants. Fluorescence reaches a steady state if the light intensity remains steady (F_t). In a light-adapted plant, effective maximal fluorescence (F_m') is lower than F_m because some of the light is being absorbed for photochemistry or dissipated as heat (non-photochemical quenching). The difference between F_m' and F_t over F_m' is the effective quantum yield of photosystem II (ϕPSII). Non-photochemical quenching (qN) = $(F_m-F_m')/F_m'$. Black arrows indicate activation of the measuring light and gray arrows indicate activation of a saturating flash.

been in dark or ambient light conditions, respectively, for at least 30 minutes before fluorometer measurements commenced.

Maximum quantum yield (F_v/F_m) is measured on dark-adapted plants and expresses the maximum efficiency of photon use by PSII (Genty *et al.* 1989). F_v/F_m is calculated as: $F_v/F_m = (F_m - F_o)/F_m$ where F_o is the minimal fluorescence, F_m is the maximal fluorescence and the difference between these two parameters is F_v, the variable fluorescence (Fig. 5.2). F_o levels were kept between 300-400 relative units for measurements of F_v/F_m (Anonymous 1993). Effective quantum yield, ϕPSII is measured on light-adapted plants and is calculated as: $\phi PSII = (F_m' - Ft)/F_m'$, where F_m' is the effective maximal fluorescence and F_t is the incident fluorescence (Fig 5.2). F_t levels were kept between 300-400 relative units for measurements of ϕPSII (Anonymous 1993).

Maximum quantum yield (F_v/F_m) and effective quantum yield (ϕPSII) are often linearly related; however, ϕPSII is measured on light-adapted plants and reflects not only the efficiency of photon use, but also the number of reaction centers open under ambient environmental conditions (Adams *et al.* 1990, Genty *et al.* 1989). If light conditions are kept favorable (i.e., intensities at which non-photochemical and photochemical quenching are balanced *sensu* Csintalan *et al.* 1999), then ϕPSII gives a similar pattern of response to induced stress as F_v/F_m (Csintalan *et al.* 1999, Lovelock *et al.* 1995, Matoušková *et al.* 1999). Therefore, ϕPSII is a good quantifier of PSII efficiency when it is impractical to dark adapt plants (Hovenden & Seppelt 1995).

Non-photochemical quenching (qN) is calculated as: $qN = (F_m - F_m')/F_m'$, where F_m is maximal fluorescence (from dark-adapted state) and F_m' is incident maximal fluorescence (from light–adapted state)(Fig. 5.2). An increase in non-photochemical quenching (qN) reflects dissipation of excess heat energy. An increase in qN in bryophytes has been associated with photoinhibition damage in light sensitive plants (Csintalan *et al.* 1999) and with a protective response during drying of plant cells in desiccation tolerant plants (Csintalan *et al.* 1999, Deltoro *et al.* 1998, Marshall & Proctor 1999, Matoušková *et al.* 1999). qN is often more responsive to changes in PSII than either measure of quantum yield (Csintalan *et al.* 1999).

Light response curves.—Species' light response curves were constructed during May and June 2000 using pieces of moss colonies with colony architecture kept in tact.

Colonies were collected from all five sites for each species over the course of the two months. On the evening of the moss colony collection day, species' responses to increasing light levels were tested through changes in ϕPSII and qN. To construct the light response curves, program "Run 8:Actinic light intensity series" on the PAM-2000 fluorometer was used. This program begins with a 10 minute adaptation period at an intermediate light intensity and goes through 10 increases in photosynthetically active light intensities (Anonymous 1993). Between saturating flashes and measurements, the program allows 6.5-minute equilibration period at the intermediate actinic light. Actual light intensities for each step varied between runs, but typically covered a range of PPF from 4 to 100 μmol m^{-2} sec^{-1} with the LED lamp and from 12 to 1200 μmol m^{-2} sec^{-1} with the halogen lamp. These intensities were high enough to detect saturation of ϕPSII in the moss samples.

Moist moss samples were placed on wet filter paper in the Walz Leaf-clip holder 2030-B. The leaf clip was used to maintain constant angle and distance from fiber optic to sample, and to measure temperature and light concurrent with yield. After the filter paper was saturated with double distilled water, the whole leaf clip including the moss was wrapped with clear plastic wrap to prevent drying of the sample during the 76-minute program run. Saturation curves were obtained from at least four colonies (each from a different site) for each species. Between species differences in the rate of yield decrease and qN saturation in response to increasing light intenstity were compared by linear regression. Light intensity was log transformed to linearize the relationships and 95% confidence intervals of the slopes were examined for overlap. Slopes with non-overlapping confidence intervals were considered statistically different at $\alpha = 0.05$.

Desiccation tolerance.—Desiccation tolerance is most often measured as the ability to recover photosynthetic activity after a drying and re-wetting event (Bewley 1995). A rehydration experiment with all six study species was performed at the University of Alberta on 15 September 2000. Colonies of all species were collected in late August and refrigerated in sealed plastic bags. On 10 September, colonies were placed in a 15°C growth chamber with a 16-hour daylight cycle at an average PPF of 12 μmol m^{-2} sec^{-1}, and 80% humidity. Plants were watered with distilled water and covered with clear plastic wrap to maintain full hydration for two days. After two days, the colonies were divided in half into a group of control plants that remained hydrated in the chamber and a group of dried plants that were uncovered and allowed to dehydrate in ambient growth chamber conditions for three days. There were three paired replicates per species.

After three days, apical fragments from the colonies were rehydrated in the leaf clip by pipetting double distilled water onto the filter paper, and effective quantum yield measurements were taken at 0, 0.5, 2, 72, 152, 202, 262, 1440 and 2880 minutes after rehydration. Yield measurements before rehydration at time zero confirmed the inactivity of treatment colonies. Measurements were taken first on treatment specimens and then on controls. Curves describing recovery of yield were fitted for each species using an equation of the same form as the Michaelis-Menten equation, which describes rectangular hyperbolic curve typical of reactions limited by a substrate, such as photochemistry by water. The curves calculated using this equation gave an empirically good fit to the data. The equation is:

$$\text{Yield} = \frac{(A^{*}\text{time})}{(B+\text{time})}$$

where yield is effective quantum yield of photosystem II, A is the asymptote, time is time after rehydration in minutes, and B is the value of x when $y = A/2$. Significant differences in coefficients for A and B were tested by comparing for overlap of their 95% confidence limits. Coefficients whose 95% confidence intervals do not overlap are considered significantly different at $\alpha = 0.05$.

The short-term (three-day) desiccation tolerance of gametophyte fragments was also tested for the four species suspected to have low desiccation tolerance. A rehydration experiment conducted on 18 June 2000 in Cadomin, Alberta compared photosynthetic recovery for samples desiccated for three days as fragments rather than as colonies. The experiment included *M. macrocarpa*, *B. pseudotriquetrum* and the two species of *Mnium* with four replicates per species. Plants were dried as fragments at ambient room temperature (20°C), relative humidity (approximately 40%), and light (PPF of approximately 10 μmol m^{-2} sec^{-1}). They were rehydrated with distilled water pipetted onto filter paper, and yield measurements were taken every 30 minutes for the first 4 hours and again after 24 hours, although only the 24 hour measurements are analysed here. Yield measurements were compared by one-way ANOVA by species. Fragment desiccation tolerance was compared with colony desiccation tolerance by two-way ANOVA by species and experiment. Species differences were determined by Tukey Post-hoc with $\alpha = 0.05$.

Long-term stress response of colonies and gametophyte fragments.

The long-term (5 month) stress response of colonies for the four species was tested under controlled growth chamber conditions. *Mielichhoferia macrocarpa* and *B. pseudotriquetrum* were not included in this experiment because of limited supply of *M. macrocarpa* colonies (i.e., its rarity). For *Didymodon* and *Mnium* species, regeneration of gametophyte fragments was compared for desiccated colonies stored from 25 May to 25 October 1999. Colonies were dehydrated at ambient room conditions (2 μmol m^{-2} sec^{-1} PPF, 20°C, 40% relative humidity) and kept under these conditions until planting. Colonies collected from the same sites in late September 1999, and kept in a growth chamber until the experiment was set up in October, were used as controls since original control colonies that had been kept in the growth chamber since May had abnormal morphology indicative of sub-optimal growing conditions. For each species and treatment, three replicates with 20 fragments were planted on 1.5% Bacto agar with Knopp's macronutrients. Planted fragments were kept in a growth chamber at 15°C and 80% relative humidity with a 16-hour daylight cycle at an average light intensity of 12 μmol m^{-2} sec^{-1} PPF. On 27 December 1999, the number of fragments that had regenerated by producing new growth was evaluated. The proportion of fragments that had regenerated were normalized by arcsine square root transformation and analyzed by two-way ANOVA for species by treatment followed by Tukey HSD post hoc test.

Long-term (3 - 4 month) stress response of gametophyte fragments was investigated by two storage treatments under field conditions. For all six species, gametophyte fragment regeneration after storage in the field dry (suspended in air) or wet (submerged in a stream) were compared after one month and one growing season. The storage site was located near the Devona Warden cabin in Jasper National Park, 53°08.8N, 118°00.6W, 1020m (see Fig. 5.1). At least 125 gametophyte fragments (plant apices without rhizoids) collected on 4-5 May 2000 were placed into 70μm pore diameter, nylon mesh bags and either submerged in a stream or suspended in air on 6 May. There were five treatments per species: 1) no storage, 2) wet storage for one month, 3) dry storage for one month, 4) wet storage for full growing season and 5) dry storage for full growing season. The no storage treatment served as a control in the sense of determining whether species regeneration differences in the storage treatments were partially a result of differences in regeneration from gametophyte fragments even without storage. Stream treatment bags were wired to the inside of a minnow trap to decrease both damage from stream detritus and the risk of loss. Air storage bags were suspended by wire and hung in a fully exposed site in close proximity to the stream where wind could blow through them. Due to slow snowmelt at higher elevations, *M. arizonicum* fragments were collected one month later than the other species, therefore while the growing season was almost four months long for all other species, it was only three months long for *M. arizonicum*.

Control fragments were planted on 7 May 2000 (7 June for *M. arizonicum*). Fragments stored for one month were planted on 7 June (7 July for *M. arizonicum*) and full growing season fragments were planted on 15 September 2000. For each species and treatment six replicates with 20 fragments each were planted onto 1.5% Bacto agar with Knopp's macronutrients and Petri dishes were sealed with Para film and stored in a growth chamber under the same conditions as the 1999 colony experiment. Some fragments had sprouted during storage in the stream and all fragments from the wet treatment were individually scored for any growth that had taken place before planting. After one month in the growth chamber, fragments were assessed for the number that produced new growth.

Fragment data were highly skewed because of high viability in control and one month treatments and no transformation could normalize the data. Non-parametric analysis was plagued by low power because of the high number of tied ranks. Therefore, parametric three-way ANOVA of species by storage time by storage condition was run and the F-values and sums of squares obtained were used as cutoffs to determine the significance of these values using a randomization test. The randomization test used the same ANOVA model and ran the model on 30,000 data sets that were randomized with respect to storage time and condition while species effect was held constant. Species effect was held constant since randomization between all cells would make the unrealistic assumption that all six moss species come from the same population (Petraitis *et al.* 2001). The randomization test was run in SAS using a program modified from Petraitis *et al.* (2001). Within species differences in fragment viability by storage condition were analyzed separately by time using ANOVA with p-value significance adjusted for multiple comparisons.

The proportion of fragments regenerating after season long storage under controlled conditions as colonies and under field conditions as fragments was compared for the species of *Didymodon* and *Mnium* that were included in both experiments. Proportions were normalized by arcsine square root transformation and compared by ANOVA.

Reproduction comparison.

Sexual reproduction allocation.— In 2000, three restricted-random 1m belt transects per species, each intersecting 50 colonies, were used to score sporophyte presence-absence on colonies of each species (150 colonies total). Sporophytes scoring in the field at the local scale allowed the same number of colonies to be scored for each species, but this approach is limited by small temporal and spatial scales. Therefore, all herbarium specimens for each species in the University of Alberta herbarium (ALTA) were also scored for the presence-absence of sporophytes. Because collections with sporophytes are more likely to be collected than those without sporophytes, this data set should offer a maximum estimate of sporophyte frequency for the study species over a wider geographic range. Both data sets were analysed by chi-square contingency tests for species differences. Tukey type multiple comparisons for proportions were performed when chi-square indicated significant species differences (Zar 1996).

Vegetative propagule regeneration.—In spring 1998, establishment plots containing fourteen gametophyte fragments each were installed at five replicate sites for each species to compare fragment regeneration between the six species. For all species, establishment plots were placed either in a position where colonies of the species were already growing, in which case the colonies and the first 2 cm of underlying substrate were removed, or in close proximity to colonies to ensure similar microenvironment. The fragments were counted from a mixture of fragments made from the stem apices of five colonies per species (one colony from each of the five sites). Fragments were hydrated during counting, but were stored dry in low light conditions. Fragments were rehydrated in the field just before planting for greater adhesion to the substrate and easier handling. All fragments were planted individually using forceps and fragments were recounted at planting time. For plot methodology, different methods had to be developed for each species because species habitats differed in substrate type (i.e., soil, rock, and wood), disturbance type (i.e., flooding, rock fall, and sheep activity) and disturbance frequency (see details below).

Species establishment plot details.— Mielichhoferia macrocarpa fragments were planted onto cement discs that were similar in pH to Cadomin conglomerate present at the largest *M. macrocarpa* population. The cement discs were made from a mixture of cement, sand and water. These plots were uniform in size (2 cm deep, 10 cm diameter) and contain the same size crevices in which to plant the fragments. *Didymodon johansenii* was planted directly onto logs where *D. johansenii* was growing. The plots were 5 cm^2 and were cleared of all organic matter before fragment planting. Pieces of nylon screening covered with native soil were used for the remaining four species. For all soil plots, the 10 cm^2 piece of nylon screening was secured with galvanized metal hooks at each corner and the soil was homogenized by crumbling between fingers and tapping firmly onto the screen.

In 1998, most of the plots for the *Didymodon* species were lost to small-scale disturbances and the data could not be analysed statistically. Therefore, new methods were developed for these species. In May 2000, plots were planted again for four out of six species, the two species of *Didymodon* and the two species of *Mnium*. *Mnium* planting methods were the same as in 1998 and serve as a control for between species comparisons. Thirty fragments were planted in each *Didymodon* plot. *Didymdon johansenii* wood plots (approximately 9 cm by 5 cm by 1 cm) were cut out *in situ* and refitted into logs before fragment planting to minimize disturbance during plot collection. All organisms present on the plot were removed by hand, plots were roughened with a nail to create crevices, and fragments were planted using the same forcep method as

1998. *Didymodon rigidulus* plots were 5cm high sections of 10cm diameter clear PVC tubing with nylon screening over one end of the tube. Soil was sifted into the plot on site and fragments were planted into the soil. All field plots analysed here remained in the field for one growing season (approximately four months) and were brought back to the University and evaluated in September of the year that they were planted. Because field experiments did not include all six species in the same year results from a growth chamber experiment are included. In 1998, a substrate experiment was performed with all six species (Cleavitt 2001) and the controls from this experiment are presented here. For all establishment experiments, the number of fragments regenerating out of the number planted were arcsine square-root transformed and compared by one-way ANOVA between species for each year. Tukey HSD was used for post-hoc mean comparisons.

RESULTS

Characterization of colony environments.

There were differences between habitats occupied by the species for water gain ($F_{5,24} = 8.19$), water loss ($F_{5,12} = 17.58$) and light levels ($F_{5,24} = 44.22$) ($p<0.001$). Moisture conditions at *Mielichhoferia macrocarpa* sites resulted in the highest water gain by the dry sponges and *D. rigidulus* sites gave the highest water loss by wet sponges and highest light levels (Fig. 5.3). Overall, sites with the greatest water gain had the lowest water loss (Pearson's $r = -1.000$, Fig. 5.3a,b). Water loss was positively correlated to habitat light levels ($r^2 = 0.710$, $p = 0.035$) suggesting that the water loss measures reflected differences in evaporation rates between the habitats.

Short-term stress responses.

In response to increasing light intensity, *M. spinulosum* was the most light sensitive species with a rapid decrease in yield and a correspondingly steep saturation of non-photochemical quenching (qN) (Table 5.1, Fig. 5.4). None of the other species differed in their short-term response to increasing light intensity. *Bryum*

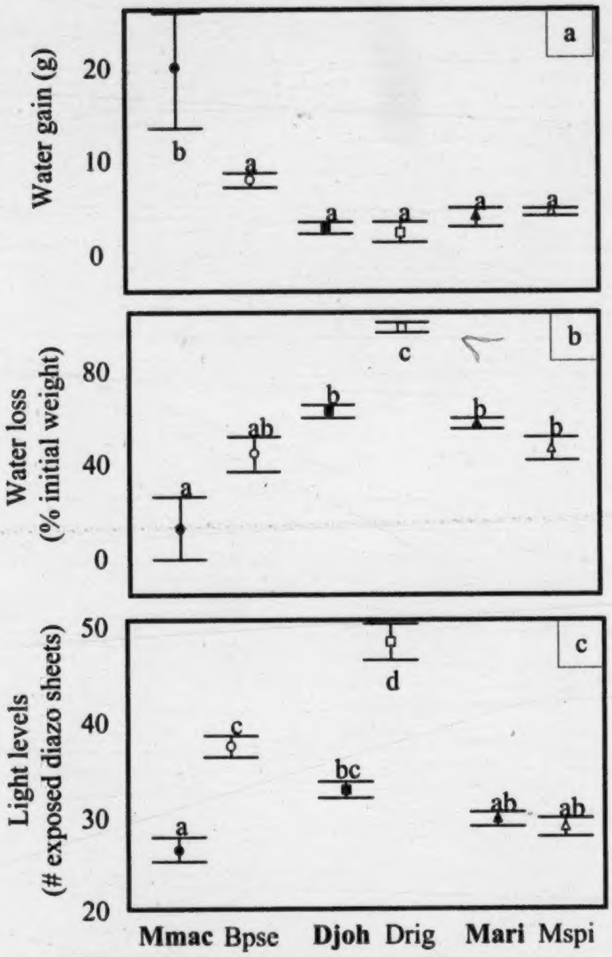

Figure 5.3. Mean values for variables comparing the habitat environment of six moss species. a) Total mean net water gain (g) of sponges placed beside moss colonies at five replicate sites per species. b) Total mean water loss (% initial wet weight) from sponges (five per site) over 5 hours during sunny days with mean temperatures above 15°C in late August 1999 at three replicate sites per species. c) Cumulative light levels measured with photo sensitive diazo blueprint paper at five replicate sites per species. Higher number of exposed sheets corresponds to higher cumulative light intensities. Means with different letters are significantly different at $\alpha = 0.05$ using Tukey HSD post-hoc test. Symbols denote the mean and error bars are standard error.

Table 5.1. Comparison of 95% confidence intervals for slopes of ϕPSII and qN responses to increasing light intensity shown in Figure 5.4 for six moss species. For the regression analysis light intensity values were log transformed to linearize the variable relationships. Slopes with non-overlapping confidence intervals were considered statistically different at $\alpha = 0.05$ and are indicated by different letter superscripts. *Mnium spinulosum* is the only species differing in it's response to high light intensities. Species names are abbreviated by the first letter of the genus and first three letters of the specific epithet. Rare species are in bold typeface.

Species	95% CI limits for % yield (ϕPSII) slope	Regression r^2	95% CI limits for qN saturation slope	Regression r^2
Mmac	-0.55 to -0.37^{b}	0.913	0.42 to 0.64^{b}	0.915
Bpse	-0.49 to -0.30^{b}	0.903	0.29 to 0.53^{b}	0.865
Djoh	-0.44 to -0.35^{b}	0.949	0.41 to 0.62^{b}	0.860
Drig	-0.52 to -0.33^{b}	0.925	0.40 to 0.53^{b}	0.956
Mari	-0.47 to -0.32^{b}	0.940	0.28 to 0.48^{b}	0.909
Mspi	-0.81 to -0.58^{a}	0.952	0.73 to 1.05^{a}	0.947

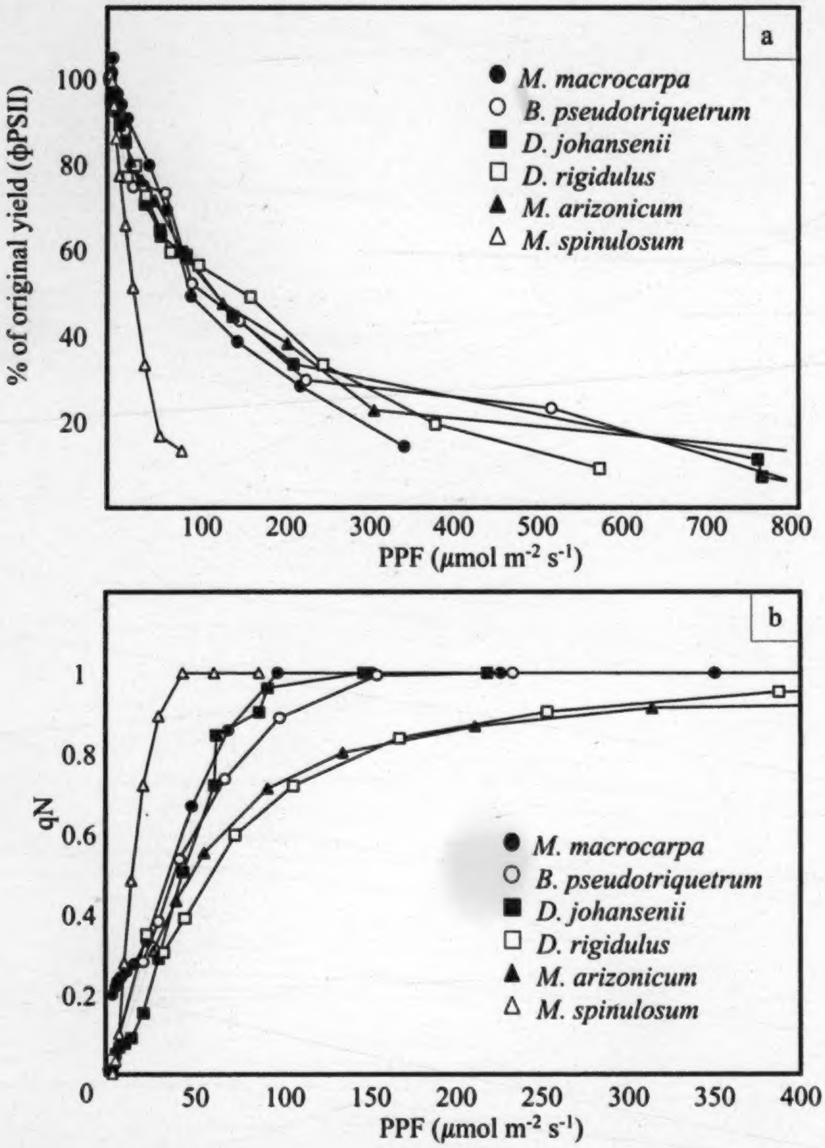

Figure 5.4. Responses of fluorescence variables ϕPSII and qN to light flashes of increasing intensities for six moss species: a) Interpolation of values for each species showing the response of ϕPSII (% of original yield) to increasing light intensities. b) Interpolation of values for each species showing response of non-photochemical quenching (qN) to increasing light intensities. Quenching potential is saturated at a value of 1.0.

pseudotriqutreum had the least desiccation tolerance as indicated by the poorest recovery of yield (Table 5.2, Fig. 5.5). The two species of *Didymodon* had the greatest desiccation tolerance (Table 5.2, Fig. 5.5). *Mielichhoferia macrocarpa* had the slowest rate of recovery while *D. johansenii* was faster than all except *B. pseudotriquetrum* (Table 5.2). After 48 hours rehydrated, four of the six species did not differ in mean yield between dehydrated and control samples (Table 5.3). *Didymodon rigidulus* had recovered mean yield significantly above the control mean and *B. pseudotriquetrum* mean recovery yield was significantly lower than the control yield (Table 5.3).

The ability to recover from desiccation was greater when plants were desiccated as colonies rather than as fragments for all four species tested (Table 5.4). Species relative desiccation tolerances were consistent between the two experiments as evidenced by lack of a significant interaction (Table 5.4). Desiccated gametophyte fragments of the four species differed in their ability to recover photosynthetic activity upon re-wetting ($F_{3,11} = 12.42$, $p = 0.001$). *Bryum pseudotriquetrum* fragments had significantly lower yield recovery (0.00±0.00) than the two species of *Mnium* (*M. arizonicum*, 0.49±0.13 and *M. spinulosum*, 0.32±0.11). *Mielichhoferia macrocarpa* fragments had lower yield recovery (0.16±0.17) than *M. arizonicum*, and the two species of *Mnium* did not differ from one another in short-term desiccation tolerance.

Long-term stress response.

Viability of gametophyte fragments differed between species, and viability differed between storage times and conditions (Table 5.5, Fig. 5.6). Differences in viability among species were not consistent between storage conditions, times or species (3-way interaction, Table 5.5). These differences were not related to differences between species viability as species viability did not differ without storage (Tukey post-hoc, $p > 0.05$, Fig. 5.6). In wet storage, all species had decreased viability after a growing season, although this effect was not different from the dry storage effect for *B. pseudotriquetrum* (Fig. 5.6). *Bryum pseudotriquetrum* was the only species that did not differ in fragment viability between dry and wet storage conditions after a growing season (Fig. 5.6). After one month, *D. johansenii* had lower viability after wet storage, while *B. pseudotriquetrum* and *M. spinulosum* had lower viability in dry storage (Fig. 5.6). After

Table 5.2. Coefficients and 95% confidence limits of equation parameters and coefficients of variation (r^2) for a non-linear regression model comparing recovery of yield after rehydration for six moss species (Fig. 5.5). The curve equation was:

$$\text{Yield} = \frac{(A*\text{time})}{(B+\text{time})}$$

where yield is effective quantum yield of photosystem II, A is the asymptote, time is time after rehydration in minutes, and B is the value of x when $y = A/2$. The asymptote here reflects completeness of yield recovery while B represents the time required for reaching half of the recovery yield. Parameters whose 95% confidence intervals do not overlap are considered significantly different at $\alpha = 0.05$ and are indicated by different letter superscripts.

Species	Recovery yield (asymptote) (95% CI limits)	Minutes to reach ½ recovery yield (B) (95% CI limits)	Regression r^2
Mmac	0.54 (0.48-0.60)^{b}	49.9 (15.3-81.4)^{a}	0.890
Bpse	0.25 (0.21-0.29)^{c}	1.78 (-0.59-4.16)^{bcd}	0.586
Djoh	0.66 (0.64-.069)^{a}	0.41 (0.28-0.54)^{d}	0.954
Drig	0.70 (0.69-0.72)^{a}	1.36 (1.05-1.67)^{c}	0.978
Mari	0.56 (0.53-0.60)^{b}	4.03 (1.67-6.38)^{bc}	0.923
Mspi	0.57 (0.55-0.60)^{b}	7.12 (3.60-10.6)^{b}	0.967

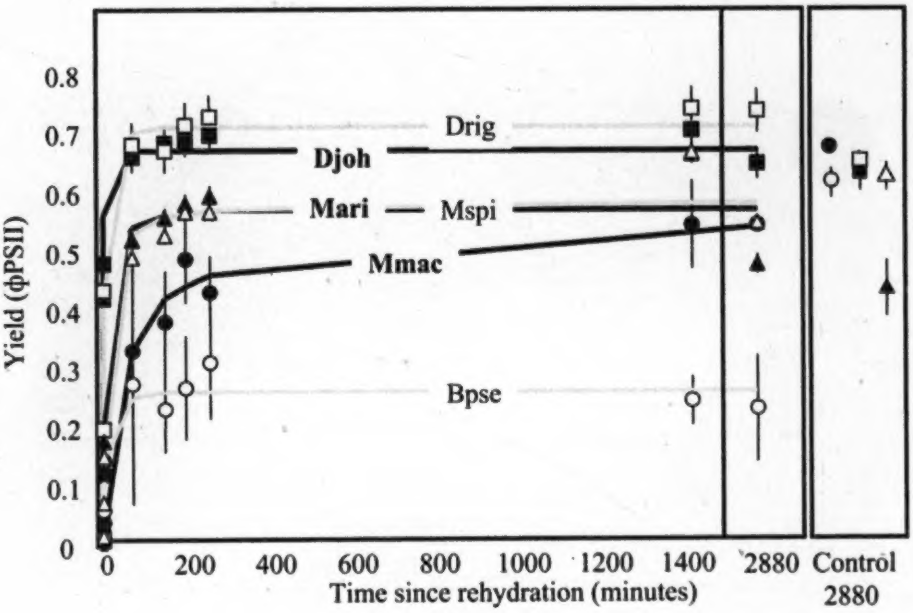

Figure 5.5. Yield (ϕPSII) recovery after 3 days of desiccation at 15°C, 20 μmol m^{-2} sec^{-1} and 80% relative humidity expressed as fitted curves for yield recovery over time. Yield recovery curves were fit with equations of the form, yield = (A*time)/(B+time), where yield is effective quantum yield of photosystem II, A is the asymptote, time is time after re-wetting in minutes, and B is the value of x when y = A/2. The control, non-desiccated sample, yield at 48 hours (2880 minutes) is presented for comparison. Species are abbreviated by the first letter of their genus and first three letters of their specific epithet. Rare species are in bold typeface and species symbols are the same as in previous figures. Symbols denote the mean and error bars are standard error.

Table 5.3. Difference between yield of dehydrated samples and yield of control samples 48 hours after rehydration of the treatment samples. Significance levels are from separate one-way ANOVA comparison of yield by species and significance levels were adjusted for multiple comparisons with ^{ns} $p > 0.008$, not significant and * $p < 0.008$.

	Yield difference	
Species	Mean (stdev)	$F_{1,4}$
Mmac	-0.13 (0.07)	9.89^{ns}
Bpse	-0.38 (0.10)	43.40*
Djoh	0.02 (0.09)	0.166^{ns}
Drig	0.08 (0.03)	34.33*
Mari	0.05 (0.11)	0.576^{ns}
Mspi	-0.07 (0.02)	8.21^{ns}

Table 5.4. ANOVA comparison of photosynthetic yield recovery 24 hours after sample rehydration between two experiments in which the same four species were desiccated as whole colonies or gametophyte fragments. Plant material was collected from the same study sites for the two experiments. Model $r^2 = 0.858$. Significance levels for F value: ^{ns} $p > 0.05$, not significant and *** $p < 0.001$.

Source	df	MS	F
Experiment	1	0.460	55.19***
Species	3	0.237	28.43***
Experiment x species	3	0.015	1.80^{ns}
Error	16	0.009	

Table 5.5. Effects of storage condition and time on fragment viability for six moss species by three-way ANOVA. (ANOVA model df = 144, $r^2 = 0.914$.). The significance of p-values was confirmed by a randomization test using 30,000 iterations. See Methods for details.

Source	df	MS	F	p
Species	5	84.69	16.7	<0.0001
Conditions	1	1128	222	<0.0001
Time	1	2017	397	<0.0001
Species x conditions	5	177.0	34.9	<0.0001
Species x time	5	41.86	8.24	<0.0001
Conditions x time	1	1620	319	<0.0001
Species x conditions x time	5	36.88	7.26	<0.0001
Error	121	5.08		

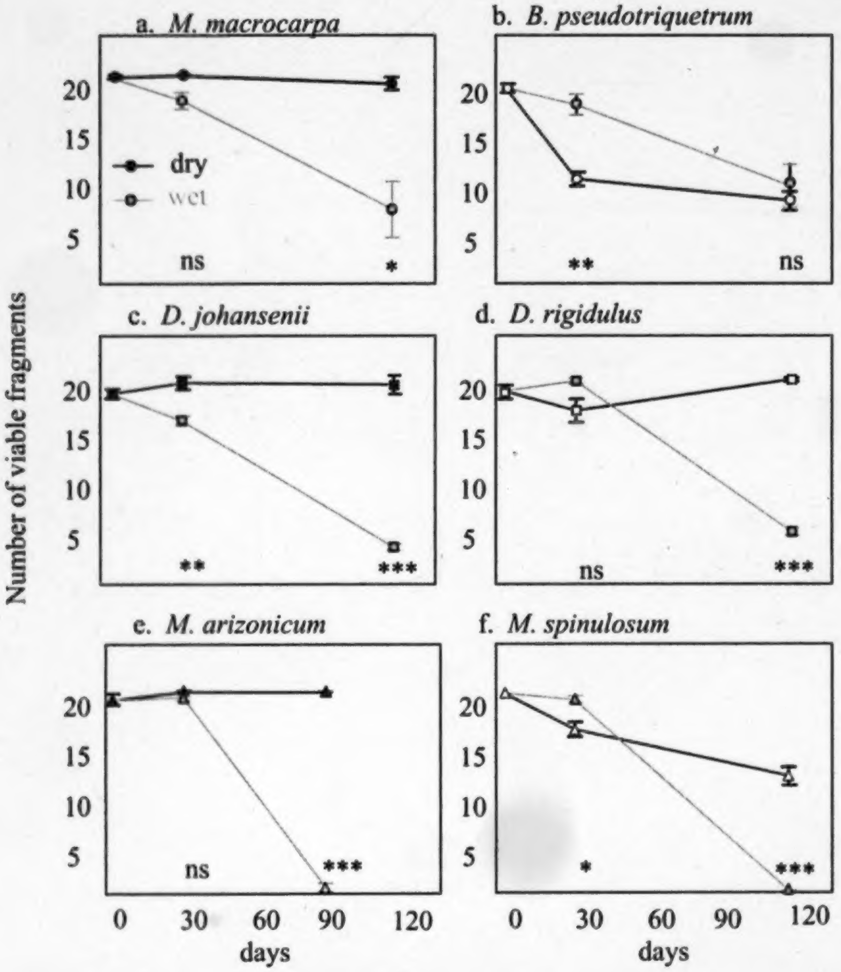

Figure 5.6. Effect of storage condition and length of storage on fragment viability for six moss species, a-f. The rare species are in bold typeface. Mean number of viable fragments (± standard error) for six replicates starting with 20 fragments each. Differences in viability between wet and dry storage for each storage time were compared by one-way ANOVA and significance levels were adjusted for multiple comparisons. These differences are shown by time above the x-axis. The significance levels are: ^{ns} $p > 0.008$, not significant, * $p < 0.008$, ** $p < 0.0017$, *** $p < 0.00017$. The same controls were used for wet and dry treatments.

a growing season stored dry, *B. pseudotriquetrum* and *M. spinulosum* had lower fragment survival than the four other species (Tukey post-hoc, $p < 0.05$, Fig. 5.6). Fragment viability after a growing season stored dry in the field was positively correlated to short-term desiccation tolerance determined by yield recovery (Pearson $r = 0.83$, $n = 6$, $p = 0.041$).

In a comparison of fragment viability following dry storage for a season as colonies under controlled conditions and as fragments under field conditions, there was a significant species by storage location interaction (Table 5.6). This interaction was due to the lack of storage location effect for three of the four species contrasting with a strong storage location effect for the fourth species, *M. spinulosum* that had much lower regeneration from fragments stored in the field (Table 5.6b).

Reproduction comparison.

Species did not vary in sporophyte frequency as scored in the field (G-test, $G = 9.19$, $df = 5$, $p>0.05$), but did as scored from herbarium specimens (G-test, $G = 15.69$, $df = 5$, $p<0.01$). The lack of between species differences in the field likely was due to overall low sporophyte frequency with no sporophyte production on scored colonies for three of the six species (Table 5.7). In herbarium specimen scoring, *M. macrocarpa* and *M. spinulosum* had the highest sporophyte frequencies (Table 5.7). *Bryum pseudotriquetrum* and *D. johansenii* were next highest, although *D. johansenii* did not differ significantly from *D. rigidulus* and *M. arizonicum* (Table 5.7).

Species also varied with respect to one another in their ability to regenerate from vegetative propagules both in the field and in the growth chamber (Table 5.8). In 1998, *M. macrocarpa* had the lowest regeneration of four species ($F_{3,16} = 16.21$, $p<0.001$, Table 5.8). In 2000, the two species of *Mnium* had higher regeneration than the two species of *Didymodon* ($F_{3,16} = 15.44$, $p<0.001$). When species were grown under controlled environmental conditions on their native substrate, regeneration from fragments was higher in *D. rigidulus* and *M. arizonicum* ($F_{5,24} = 51.62$, $p<0.001$), and *M. macrocarpa* had the lowest regeneration of all six species (Table 5.8).

Table 5.6. ANOVA comparison of fragment viability in two experiments where four moss species were stored for four months under dry conditions as fragments in the field or as colonies indoors. The indoor location had less variable overall environment and lower light levels than field location.

a) Two-way analysis of species by environment effects on propagule viability. Significance levels are: ^{ns} $p > 0.05$, not significant and *** $p < 0.001$.

Source	df	MS	F
Experiment	1	0.009	0.52 ^{ns}
Species	3	0.475	27.55***
Experiment x species	3	0.133	7.70***
Error	36	0.017	

b) One-way analysis of experiment effect separated by species with significance levels adjusted for multiple comparisons: ^{ns} $p > 0.0125$, not significant, * $p < 0.0125$, ** $p < 0.0025$, *** $p <0.00025$,.

Species	MS	$F_{1,4}$
Djoh	0.002	0.08^{ns}
Drig	0.027	1.37^{ns}
Mari	0.065	6.83^{ns}
Mspi	0.313	28.3**

Table 5.7. Differences in species sexual reproductive allocation as expressed by sporophyte production. Field data were gathered from 150 colonies per species within the study area, each scored for the presence/absence of sporophytes. All herbarium specimens in ALTA (University of Alberta) for each species were also examined for presence/absence of sporophytes. Proportions that were not significantly different at $\alpha =$ 0.05 in a Tukey-type multiple comparison test have the same letter superscript.

	Field			Herbarium		
Species	# of colonies scored	sporophytes	%	# of collections examined	sporophytes	%
Mmac	150	16	10.7^{a}	12	12	100^{c}
Bpse	150	0	0^{a}	319	142	44.5^{b}
Djoh	150	15	10.0^{a}	12	4	33.0^{ab}
Drig	150	0	0^{a}	86	18	20.9^{a}
Mari	150	0	0^{a}	59	5	8.5^{a}
Mspi	150	56	37.3^{a}	171	151	88.3^{c}

Table 5.8. Percent of fragments that regenerated under field and chamber conditions for six moss species. All species were planted in 1998; however, missing data signify that the majority of plots for that year were lost to disturbance (see Methods). Species means that are significantly different between species within a column at $\alpha = 0.0125$ using Tukey Post-hoc have different superscript letters. For field data, mean fragment regeneration (three plots per site) at the same five replicate sites per species are reported. Chamber data are the means of five replicates from controls of data presented in Cleavitt (2001).

	Field		Chamber
Species	1998	2000	1998
Mmac	14.2 (14)^{a}		8.00 (6.7)^{a}
Bpse	81.8 (10)^{b}		67.0 (17)^{b}
Djoh		14.2 (16)^{a}	81.0 (17)^{bc}
Drig		27.3 (18)^{a}	99.0 (2.2)^{d}
Mari	66.6 (25)^{b}	92.9 (6.9)^{b}	100 (0)^{d}
Mspi	73.2 (10)^{b}	83.1 (13.1)^{b}	95.0 (6.1)^{cd}

DISCUSSION

Adult physiology and habitat characteristics.

Several authors have suggested that rare species are rare because they have narrower fundamental niches (i.e., narrower physiological tolerances) than common species (Cain 1940, Stebbins 1942, Brown 1995, Rosenweig & Lomolino 1997). The results of this rare-common species comparison for mosses directly contradict the expectations of this theory. Two out of three of the common species, *M. spinulosum* and *B. pseudotriquetrum,* were found to have physiological limitations that related to the habitat they occupy whereas none of the rare species displayed such limitations. *Mnium spinulosum* was the only species sensitive to high light intensities and it did grow in sites with low light levels (Table 5.1, Fig. 5.3), and *B. pseudotriquetrum* was desiccation intolerant and occurred in sites adjacent to streams that tended to be moister than sites occupied by the other species, except those of *M. macrocarpa* (Fig. 5.3). In a previous study (Cleavitt 2001), *D. rigidulus* and *M. macrocarpa* were found to be physiologically limited to calcareous substrates. Therefore, physiological limitations have been documented for all three common species and only one of the rare species. Physiological limitations of common species may be easier to detect if they occupy a higher proportion of the habitats where they are physiologically capable of living than rare species, i.e. if their realized niches more closely reflect their fundamental niches. The lack of correspondence between physiological capabilities and observed habitat occupation for the rare species suggests that their realized niches reflect limitations imposed by processes such as competition and/or dispersal.

Two of the rare species, *M. macrocarpa* and *D. johansenii*, occur in darker, more mesic habitats than their common species pair. Sites where these two rare species occur have relatively lower physiological stress than sites characteristic of their non-rare counterparts. This should allow for greater productivity in the rare species, since for bryophytes differences in productivity ultimately depend on differences both in the amount of time spent in a metabolically active state and in physiological efficiency during that time. Monitoring of colony expansion over three years and *in situ* chlorophyll fluorescence measurements both support the idea of higher productivity by *M.*

macrocarpa and *D. johansenii* relative to their common counterparts (Cleavitt, Chapter 6). All bryophytes are only metabolically active when wet (Proctor 1999). They are adapted for physiological activity in mesic, shaded conditions (Alpert & Oechel 1985, Proctor 1999). Based on the effects of desiccation on nutrient uptake and biomass increase in two moss species, Bates (1997) concluded that highly productive bryophytes must spend continuous, extended time hydrated and metabolically active. Therefore, these two rare species may be limited to habitats where they can maintain high physiological efficiency. The question then becomes why don't the common species out-compete the rare species in these habitats? Perhaps it is because the rare species only occur in environments where they are capable of being the top competitors.

The third rare species, *M. arizonicum*, may represent a different type of rarity than *M. macrocarpa* and *D. johansenii* as evidenced by its endemism, relatively high establishment potential (Cleavitt 2001, i.e. Chpt. 3), and lack of habitat distinction from its common species pair (Fig. 5.3). The physiological comparison between the endemic, *M. arizonicum*, and its holarctic congener, *M. spinulosum*, revealed no differences between the two species that explain the more restricted distribution of *M. arizonicum*. In a comparison of a vascular cedar glade endemic, *Echinacea tennesseensis*, and its widespread congener, *E. angustifolia*, there was also a lack of physiological differentiation between the two species (Baskauf & Eickmeier 1994). Partly based on this outcome, *E. tennesseensis* was concluded to have a distribution reflecting the effects of historical rather than autecological factors (Baskin *et al.* 1997). Historical factors, such as mountain building and glaciation, may also be important in the case of the two species of *Mnium*. However, the implications of autecological differences such as sporophyte frequency and, therefore, dispersal ability in *M. arizonicum* relative to *M. spinulosum* remain to be investigated. Overall, the differences or similarities in ecological limitations of the three rare species relative to one another were reflected by the differences or similarities in their geographic distributions. *Mielichhoferia macrocarpa* and *D. johansenii* have widely disjunct geographic distributions, and both lack physiological limitation to source environment and have low regeneration. *Mnium arizonicum* is geographically restricted to North America and does not have clear ecological limitations at the local scale. The idea that disjunct and endemic species often have different causes of rarity (Fiedler & Ahouse 1992) is supported by the results of this study.

Early hypotheses of a narrow physiological tolerance of rare species were largely based upon observations of rare species habitat characteristics (e.g., Cain 1940, Stebbins 1942). The results of this study emphasize that the temptation to infer physiological tolerance from habitat characteristics should be avoided. For instance, *M. macrocarpa*, a rare moss that occurred in the wettest, darkest sites, was not found to be physiologically limited by either desiccation tolerance or light levels in this study. This finding is somewhat counter-intuitive given that there is ample evidence for correspondence between habitat moisture regime and bryophyte desiccation tolerance (Brown & Buck 1979, Seel *et al.* 1992, Oliver *et al.* 1993, Deltoro *et al.* 1998, Csintalan *et al.* 1999, Robinson *et al.* 2000). This departure from the usual relationship between habitat and desiccation tolerance may be explained if habitat moisture regimes are more rigorously classified. For instance, although *M. macrocarpa* occurs at sites that are hydric throughout the growing season, these sites dry out in autumn when the seep water freezes and remain dry without protection from snow cover until late spring/early summer (pers. obs.). Therefore, this species would be expected to possess some type of desiccation tolerance.

There are two types of desiccation tolerant plants, poikilochlorophyllous and homoiochlorophyllous, and both types occur in bryophytes (Tuba *et al.* 1998). Poikilochlorophyllous bryophytes experience breakdown of their chlorophyll in response to drying-wetting cycles and survive in habitats that are generally mesic and slow drying such that drying-wetting cycles tend to be both longer in duration and less frequent (Oliver *et al.* 1998, Tuba *et al.* 1998). Homoiochlorophyllous bryophytes retain their chlorophyll through drying-wetting cycles and occupy more xeric, exposed habitats that experience more frequent, brief, rapid drying events; however, even for these mosses fast desiccation leads to a prolonged recovery period (Oliver *et al.* 1998). Therefore, the frequency, rate and duration of habitat drying throughout the year are important in accurately describing the relationship between desiccation tolerance and moss habitats (Oliver *et al.* 1993, Oliver *et al.* 1998, Tuba *et al.* 1998). Based on the facts that *M. macrocarpa* is desiccation tolerant and that it occurs in habitats which dry out infrequently for long periods of time, this moss is most likely poikilochlorophyllous. This hypothesis is also supported by *M. macrocarpa*'s relatively slow rate of recovery in photosynthetic yield after rehydration (Fig 5.5, Table 2.2).

Propagule physiology, adult habitat characteristics and potential dispersal vectors.

The match between vegetative propagule physiology and adult habitat environments varied between the six species and within species over time. The lack of perfect correlation between habitat moisture and fragment survival following dry storage agrees with Dalen and Söderström (1999), but there is evidence of a correspondence between habitat moisture regime and ability for long distance dispersal via wind for spores (van Zanten & Gradstein 1988). As with adult physiology, there may be a clearer relationship with habitat moisture regimes and vegetative fragment physiology once moisture regimes are quantified more rigorously. More experiments designed to discover the relationship between dispersal time and distance dispersed are necessary before a more biologically meaningful assessment of dispersal can be achieved via storage treatment experiments. In particular, the biological significance of fragment viability after one month versus four months is currently unclear. Therefore, storage experiments are most informative in terms of ruling out potential dispersal vectors, such as water versus air, rather than describing dispersal ability.

For example, *B. pseudotriquetrum* had the highest potential for fragment transport in water and the lowest for air transport. It is the only species in this study observed to grow in seasonally flooded habitats and to disperse effectively via streams. In two out of three seasons when establishment plots were setup for this species, the majority of the plots were completely flooded and consequently contained not only a new layer of silt, but also naturally dispersed gametophyte fragments of *B. pseudotriquetrum* that proceeded to grow in the plots. *Mielichhoferia macrocarpa* had higher fragment viability after storage in air rather than water after four months, but there was no difference between fragment viability in air versus water after only one month. The likelihood of water transport for this species depends on the number of vertical rock seeps encountered by a waterway along which it occurs. The unexpected high viability of fragments stored dry makes transport by wind, especially during the winter, another plausible mode of asexual dispersal for *M. macrocarpa*.

Didymodon johansenii is the third species that lives in sites disturbed by flooding. During 1997-2000, one of nine *D. johansenii* sites was flooded (pers. obs.). Although propagule viability for *D. johansenii* fragments was lower in water than in air after one month, 80% of fragments were still viable after one month in water (Fig. 5.6). In Alberta, flooding of *D. johansenii* sites may be ecologically significant for this species since fine silt deposited by flooding has been shown to increase chances of fragment establishment by increasing fragment adherence to logs (Chpt 4). Therefore, fragments deposited in wet silt may have a much higher establishment rate than fragments deposited by other vectors. The ability of *D. rigidulus* to survive submergence for one month with no difference between fragment viability stored dry versus wet, is somewhat incongruent with the habitat environment described in this study. However, the *D. rigidulus* complex contains many varieties capable of living in varied habitats (Zander 1998, Kučera 2000) and it may be that the ability to survive submergence is an ancestral trait in the complex (Zander 1998).

Based on differences in viability after growing season storage, dispersal by air, either in wind or on animals, is the most likely dispersal path for fragments of all species except *B. pseudotriquetrum*. Dispersal of vegetative moss fragments by both invertebrates (Gerson 1982, van Tooren & During 1988) and vertebrates (Kimmerer & Young 1996) has been observed. Kimmerer and Young (1995, 1996) have experimentally demonstrated the physical potential for dispersal of asexual propagules via chipmunks and slugs. Animal dispersal may be an important vector particularly for *D. johansenii*, *M. arizonicum*, and *M. spinulosum* that grow in sites with high red squirrel traffic. *Mnium arizonicum* has frequently been noted growing at the entrance to squirrel holes under spruce and fir trees in the sub-alpine (pers. obs.). *Didymodon rigidulus* colonies also experienced animal disturbance by ants, grasshoppers, and bighorn sheep. Carefully planned experiments will be needed to test these observationally based hypotheses. The dispersal ecology of bryophytes remains skewed toward spore dispersal studies (e.g., van Zanten & Pócs 1981, van Zanten & Gradstein 1988, Marino 1991), and more studies on gametophyte fragment dispersal are needed.

Concurrence of stress responses.

The main stress responses investigated in this study were high light tolerance, short-term (3-day) desiccation tolerance, and tolerance of vegetative propagules to desiccation or submergence. Short-term desiccation tolerance and vegetative propagule desiccation tolerance were positively correlated in this study. The two species of *Didymodon* and *M. arizonicum* had high desiccation tolerance in both cases while *B. pseudotriquetrum* had low desiccation tolerance in both experiments. For species like *B. pseudotriquetrum* that are desiccation intolerant, overland dispersal by gametophyte fragments becomes more unlikely (Figs. 5.5, 5.6) and colonization events between unconnected streams would require spore dispersal. *Mnium spinulosum* exhibited sensitivity to high light intensities both in short-term light response and long-term decreased propagule viability. Intolerance of high light conditions rather than short-term desiccation tolerance may limit the vegetative dispersal of this species and dispersal between forested areas likely requires spores. Not all types of desiccation tolerance infer high light tolerance, and it may be only in homoiochlorophyllous species that physiological changes in preparation for desiccation confer protection from photodamage.

Propagule viability and reproductive strategy.

Propagule viability differed among the six species; however, fragment viability and ability to regenerate from gametophyte fragments did not coincide for all six species. The two species with the lowest sporophyte production, *Mnium arizonicum* and *D. rigidulus*, had the highest propagule viability in three out of four treatments (Fig. 5.6). *Mnium spinulosum* and *M. macrocarpa* had the highest sporophyte frequency (Table 5.7), but only *M. spinulosum* displayed lower fragment viability than *M. arizonicum* or *D. rigidulus* (Fig. 5.6). Therefore, although there is evidence that species with lower sporophyte production have high fragment viability, there is no evidence from this study that species with high sporophyte production have relatively lower fragment viability. There was also no clear relationship between fragment viability measured in this study and ability of the six species to establish from fragments in the field or chamber. In particular, *M. macrocarpa* had low establishment from fragments both in the field and chamber (Table 5.8), but high fragment viability in three out of four treatments (Fig. 5.6). In contrast, *B. pseudotriquetrum* had high establishment in the field (Table 5.8) and low fragment viability in three out of four treatments (Fig. 5.6). The discrepancy between fragment viability and fragment establishment ability suggests separation of dispersal and establishment limitations for some species. This functional separation means that dispersal potential does not automatically equate with the ability to compete for habitat space. In addition, the inference of dispersal limitation should not automatically be made from low occupation of suitable habitats (eg. Söderström 1989) since this distribution pattern could also arise from an establishment limitation.

In recent synthetic studies of rare and common species traits, rare species tend to have higher asexual and lower sexual reproductive potential than common species (Gaston & Kunin 1997), and these trends appear to apply to bryophytes (Hedderson 1992, Longton 1992). Rare-common species comparative studies on flowering plants support the trend of lower sexual reproductive output (i.e., seed set) in rare versus common species; however, the pattern of higher asexual reproductive success is less consistent (e.g., Banks 1980, Morley 1982, Fiedler 1987, Byers & Meagher 1997). Although it represents a very small sample size, this study is the first experimental comparison of the asexual reproductive potential of rare and common moss species. Overall, the rare species had greater asexual reproductive potential than the common species with two out of three rare species having higher fragment viability after dry storage than their common species pairs for both time periods (Fig. 5.6). The ability for asexual propagation has previously been correlated to sexuality in mosses with dioicous (unisexual) species more likely to produce asexual propagules than monoicous (bisexual) species (Schuster & Longton 1983). The results of this study support this pattern in the sense that *M. spinulosum* and *B. pseudotriquetrum*, the only study species that are monoicous (although *B. pseudotriquetrum* can also be dioicous) were also the study species to have lowest fragment viability after dry storage (Fig. 5.6).

Conclusion.

The three common species in this study demonstrated physiological limitations that relate to their habitat occupation, while this was true for only one of the rare species. This intriguing trend suggests that relative to rare mosses, the realized niches of common mosses more fully reflect their fundamental niches. That is, common mosses occur in more of the sites that they are physiologically capable of occupying. In general, physiological limitations should not be concluded for a species solely based on observations of narrow habitat characteristics. Differential vegetative propagule viability within and between species after different storage treatments could be logically related to habitat characteristics of adult plants. However, quantification of habitat moisture regimes requires greater differentiation than the simplistic hydric to xeric classification. Overall, interpretation of propagule viability studies are somewhat limited by lack of knowledge on the relationship between dispersal time and distance dispersed.

Short-term desiccation tolerance and long-term vegetative propagule viability after desiccation were closely correlated for species in this study. However, desiccation tolerance did not always correspond to high light tolerance and this correspondence may be limited to homoiochlorophyllous species. Frequency of sporophyte production did not correspond to fragment viability or ability of fragments to establish. In addition, fragment viability and fragment establishment ability were not related for a given species. Variation in regeneration by vegetative propagules suggests that differences in reproductive ability between moss species are complex and should not be inferred solely from differences in sporophyte frequency. The relationship between sporophyte frequency, spore dispersal ability and spore establishment ability needs to be explored. Similarly, both dispersal and establishment limitations could lead to low occupation of "suitable" sites and these are functionally separate autecological limitations.

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Chapter 6: Local persistence of three rare and three common moss species explored through establishment experiments, reciprocal transplants, and colony mapping

Species differ substantially in range sizes and many studies suggest that ecological limitations at the local scale can, in large part, explain these differences (review by Brown *et al.* 1996, Thompson *et al.* 1998). In particular, differences in realized niche breadths (also termed ecological amplitudes) of species may be an important trait differentiating rare and common species (Shaw 1981, Brown 1984, 1995). Species with a relatively narrow realized niche (*sensu* Hutchinson 1957, Austin *et al.* 1990) are often termed habitat specific with habitat specificity differences considered a defining trait of rare species (*sensu* Rabinowitz 1981). Much evidence in support of this pattern has led to the "habitat hypothesis", which argues that rare species are rare because they are restricted to rare habitats (Prober & Austin 1990), and the related "resource availability theory", which states that rare species use resources that are rare (Hanski *et al.* 1993). While the "habitat hypothesis" does not specify the reason for habitat restriction, the "resource availability theory" suggests that rare abiotic resources are limiting the distribution of rare species. The factors responsible for habitat specificity, a.k.a. narrow realized niches, can be varied and complex, but almost always include a distinction between abiotic and biotic influences (Hutchinson 1957, Austin *et al.* 1990). This distinction is often made via an assessment of species response to habitats where they are naturally present, "native", versus absent, "non-native" (e.g., Alpert 1988, Frego & Carleton 1995, Mulligan & Gignac 2001).

One explanation for a species having a narrow realized niche would be if the species also had a narrow fundamental niche as suggested for rare species by Brown (1995). A prior study of six moss species suggested that the three rare species studied were not limited in distribution by having smaller fundamental niches than common species, yet each of the three rare species studied are, in fact, restricted to specific habitats on the landscape (Chpts. 2 & 5). Alternative hypotheses for their habitat specificity tested here are: 1) the three rare species are restricted to these habitats during the establishment stage, which accounts for association with these (non-successional) habitats in latter stages (Harper *et al.* 1961, Grubb 1977), and 2) the rare species are restricted in adult stages not by absolute physiological tolerance, but by physiological restrictions imposed by neighbor interactions (Krukeberg 1951, Robson & Maze 1995). That is, the species must grow in environments where they can maintain competitive growth rates and/or in environments were there is less competition for space from other species. Some studies (Lusk & Smith 1998, Antonella *et al.* 1999) have also shown that consideration of limitations 1) and 2) together best explains species distribution patterns.

The relevance of establishment ability and growth rates to site occupation may vary between species depending on differences in the occurrence of colony disappearance and neighbor interaction at these sites (Grime 1979, Grubb 1977, 1988). In sites that experience higher disturbance resulting in higher colony disappearance, species may have fewer neighbor encounters and are less likely to be limited by growth rates than by establishment ability (Grime 1979). Establishment ability is defined here as the ability of propagules to adhere to a substrate and to expand by vegetative growth in that site without necessarily reaching a stage of gametangial production. Limitations in the establishment stage could be evidenced by relatively low overall establishment ability or by higher establishment ability in native sites and/or sites without neighbors (Reader & Buck 1986, Goldberg 1987, Mark *et al.* 1995, Kotorová & Lepš 1999). Higher establishment of rare species in native sites would support both the "resource availability hypothesis" and the "habitat hypothesis", while low establishment in the presence of neighbors would support the "habitat hypothesis" only (Prober & Austin 1990, Hanski *et al.* 1993). Overall low establishment pertains more to the "vital rates theory" that suggests rare species are rare because of differences in demographic parameters such as recruitment (Holt *et al.* 1997).

Differences in bryophyte establishment ability may correspond with life history strategies (*sensu* During 1992)(Miles & Longton 1990) or they may explain local distribution patterns of colonies (Kimmerer 1991, 1994, Mc Alister 1995, Li & Vitt 1994, 1995, Kimmerer & Young 1996). Competition in the establishment stage may be more important than competition in the adult stage for a number of plant forms including trees

(Lusk 1995, Anderson & Winterton 1996, Kubota & Hara 1996), shrubs (Davis 1991), herbs (Howard & Goldberg 2001), and bryophytes (Watson 1981, Li & Vitt 1994, 1995).

In bryophytes, competition is thought to occur mainly for space (Marino 1991, Rydin 1995, 1997a,b, Slack 1997) and can limit colony growth and expansion. O'Connor (1987) proposed a "habitat selection theory" emphasizing the importance of neighbor interaction in causing rare species to have narrower realized niches. If rare species can only occur where competition is less intense or where they are better competitors, then rare plants should have fewer neighbor encounters and/or higher growth rates and fewer losses in neighbor interactions. This study examines establishment ability and growth of six moss species at native and non-native sites, and compares colony growth, disappearance and neighbor interactions for these species at native sites. As the importance of competition may vary with habitat disturbance regime (Grime 1979, Tilman 1982), the relationship of neighbor encounter frequency to disturbance regime is considered. Proximal limitations to local distribution are discussed for the six species with reference to rarity theory and plant strategy theory.

METHODS

Study species & sites.

Species selection criteria are detailed in Cleavitt (2001). The three species pairs, with the rare species listed first, are *Mielichhoferia macrocarpa* (Hook) Jaeg. and *Bryum pseudotriquetrum* (Hedw.) G.M.S., *Didymodon johansenii* (Williams) Crum and *Didymodon rigidulus* Hedw. var. *gracilis* (Schleich.) Zand., and *Mnium arizonicum* Amann and *Mnium spinulosum* Bruch & Schimp. *Didymodon rigidulus* var. *gracilis* will be referred to as *D. rigidulus* throughout the rest of this paper. Establishment and competitive abilities of these species are unexplored. *Mnium spinulosum* and *D. johansenii* have been observed to regenerate from vegetative fragments (Lersten 1961, Kuc 1973, respectively). However, there is no documentation in the field of establishment by these six species.

The species differ in traits that may relate to differences in competitive abilities such as stem and colony sizes and percent cover at a site (Chpt. 2). *Bryum* *pseudotriquetrum* has larger stems and colonies than *M. macrocarpa* and also tends to have higher percent cover at sites where it occurs (Chpt. 2). *Didymodon johansenii* has smaller stems than *D. rigidulus*, but larger average colony sizes. Because of patchier colony distribution within a site, *D. johansenii* tends to have lower percent cover of sites where it occurs than *D. rigidulus* (Chpt. 2). *Mnium arizonicum* and *M. spinulosum* have stems that are equivalent in size and *M. arizonicum* has larger colonies. *Mnium arizonicum* is more patchily distributed within a site and covers a lower percentage of site area (Chpt. 2).

Study sites are located in the eastern Front Ranges and Foothills of the Canadian Rocky Mountains, Alberta, Canada, mainly within Whitehorse Creek Wildland Park and Jasper National Park. Sites for *M. macrocarpa*, *B. pseudotriquetrum*, and *M. arizonicum* are located largely within the Whitehorse Creek Wildland Park (1600-2000m). *Mnium spinulosum* sites are located at lower elevations, 1400-1410m, in the Rocky Mountain foothills ecoregion on Weldwood of Canada Ltd. property along Cold Creek Road. *Didymodon johansenii* and *D. rigidulus* sites are located at the lowest elevations (1050-1150m) in the montane ecoregion of Jasper National Park. In 1998, five replicate sites were established for each species. A sixth site per species, in the same general area, was used for collecting transect data in 2000 (see Chpt. 2, Fig. 2.2, Table 2.3).

Establishment ability.

Hypotheses concerning habitat restrictions imposed during the establishment stage were tested by establishment experiments using gametophyte fragments of the species. Fragments consist of the apical portion of the plants with no sporophytes or rhizoids attached. Fragment size was uniform within a species, but varied between species because of variation in overall plant sizes (Chpt 2, Fig. 2.1). There were three sets of establishment experiments: 1) establishment alone for four months at native sites, 2) establishment alone at native and non-native sites (time period varies by species pair), and 3) establishment with and without neighbors. Establishment ability of all six species was compared after 4 months to assess overall establishment ability. Comparisons between paired rare and common species were made for the effect of site (native versus non-native) and/or presence of neighbors on establishment. Species pairs varied in the number of within species hypotheses that could be tested due to differences in plot disturbance and methodology. Because species habitats differed in substrate type (i.e., soil, rock, and wood), disturbance type (i.e., flooding, rock fall, and sheep activity) and disturbance frequency, different establishment methods had to be developed for most species. General establishment plot methods are given in Chapter 5 and differences in plot type are outlined in Table 6.1 and under "species details" below. Establishment (proportion of fragments regenerating of those planted) was separated into two components, recovery (proportion of fragments found of those planted) and regeneration (proportion of fragments regenerating of those found). Recovery reflects fragment disappearance while regeneration is a minimum estimate of ability for fragments to regenerate since the fate of unrecovered fragments is unknown. Missing plots or plots destroyed by animals in the field were entered as zeroes in terms of fragment recovery and as empty cells in terms of fragment regeneration. All proportions were arcsine-square-root transformed before ANOVA analysis. Planned comparisons were made on establishment at native versus non-native sites for each species (Sokal & Rohlf 1981).

Species details.—Methodological adjustments for four-month, native site plots are explained in Chapter 5, and native versus non-native and neighbor plot details are described here. *Mnium arizonicum* and *M. spinulosum* plot types were the same as described in Chapter 5 for all experiments as no adjustments were necessary to mitigate plot disturbance. Native and non-native plot types for *M. macrocarpa* and *B. pseudotriquetrum* are the same as 1998 native sites, and the native site plots were the same plots in both experiments. The native and non-native site plots for *D. johansenii* and *D. rigidulus* were set up in 1999 (Table 6.1). At *D. rigidulus* sites, *D. johansenii* fragments were planted onto pieces of wood transported from *D. johansenii* sites and secured with wire to the ground. The plots were standardized to the same size as plots cut at the native *D. johansenii* sites and sat flush with the ground. *Didymodon rigidulus* was planted using similar methods to the one-season native plots in 2000 (Chpt. 5), except 10cm diameter plastic dishes with drainage holes were used instead of the PVC pipe with screening. This methodology switch resulted from concerns over photo-

Table 6.1. Outline of establishment plot methodology by species and treatment. Reasons for changes in methodology are discussed in the methods section of this chapter and chapter 5. Methodology for *M. arizonicum* and *M. spinulosum* remained unchanged from methods described in Chapter 5 and these two species are not included here. *M. macrocarpa*, *B. pseudotriquetrum*, *D. johansenii* and *D. rigidulus* are abbreviated by the first letter of their genus and first three letters of their specific epithet. The rare species are in bold.

Species	Treatment	Year(s)	Plot type	# fragments per plot
Mmac	4 mo., native	1998	cement discs	14
	4 mo., non-native (Bpse)	1998	cement discs	14
	4 mo., native, neighbors	1999	glass vials	15
Bpse	4 mo., native	1998	soil screens	14
	4 mo., non-native (**Mmac**)	1998	soil screens	14
	4 mo., native, neighbors	1999	glass vials	15
Djoh	4 mo., native	1998	directly on logs	14
	4 mo., native	2000	pre-cut log plots	30
	16 mo., native	1999-2000	pre-cut log plots	15
	16 mo., non-native (Drig)	1999-2000	pre-cut log plots	15
Drig	4 mo., native	1998	soil screens	14
	4 mo., native	2000	PVC w/ screen bottom	30
	16 mo., native	1999-2000	plastic dish w/ holes	15
	16 mo., non-native (**Djoh**)	1999-2000	plastic dish w/ holes	15

degradation of the plastic dishes observed during the 1999 field season. The PVC plots were more durable and resistant to photo-degradation damage; however, the plots were functionally very similar. The sides of the plastic dishes were 2.5cm high and effectively minimized overgrowth of the plots by forest floor species at *D. johansenii* sites, and slippage of plot soil and contents at *D. rigidulus* sites. The plots were anchored by four pieces of 16 gauge galvanized wire stuck through the bottom of the dishes and into the ground.

The effect of neighbor presence was tested for *M. arizonicum* and *M. spinulosum* at both native and non-native sites, and for *M. macrocarpa* and *B. pseudotriquetrum* at *M. macrocarpa* sites only due to logistical constraints imposed by repeated severe flooding of *B. pseudotriquetrum* sites in 1999 (Table 6.1). In 1999, plots for *M. macrocarpa* and *B. pseudotriquetrum* were planted into clear 30ml glass scintillation vials to mitigate flooding disturbance experienced on 1998 plot types (Table 6.1). The vials contained silt from the site so that both species were growing on the same substrate unlike the 1998 plots where *M. macrocarpa* was on cement discs and *B. pseudotriquetrum* was on soil plots. The vials were left uncapped and laying on their sides perpendicular to water flow down the cliff. Because this method reduced disturbance rate, differences in fragment recovery were not considered. There were three sets of vials with three vials in each set (nine vials per site). In each vial, the first set had 15 fragments of *M. macrocarpa* only, the second had 15 fragments of *B. pseudotriquetrum* only, and the third had 15 fragments each of both species. The neighbor plots for *M. arizonicum* and *M. spinulosum* contained the same number of fragments. Therefore, density effects were not separated from intraspecific competition effects in these experiments. There were no neighbor plots set up for the *Didymodon* species as they were the only species pair not observed to naturally occur together at the same site.

Colony growth and disturbance.

Colony performance was quantified by comparing short-term photosynthetic efficiency as measured by chlorophyll fluorescence yield measurements and by measuring colony growth after three years. Monitoring of colonies over three years also allowed scoring of colony disturbance. In 1998, at least 50 colonies were mapped and measured (length of longest axis and perpendicular to longest axis) at three of the five sites per species. Colony photographs were taken for at least 36 colonies at each site at the time of mapping during the 1998 season. In 2000, colony size was re-measured and colonies were scored for changes in size. The main scoring for size change was: 0) disappeared, 1) decreased size, 2) size unchanged, 3) increased size. Based on 1998 photographs, size decreases resulted from partial disappearance or death of colony patches and overgrowth by neighbors. Colony scores for growth and disappearance were compared by chi-square contingency analysis and Tukey-type post-hoc test for multiple comparisons of proportions (Zar 1996, pg. 561). All species data sets were checked for independence of sites by chi-square and site data were pooled before analysis.

Short-term photosynthetic efficiency was measured by chlorophyll fluorescence using a pulse amplitude modulation (PAM) fluorometer (Walz, Effeltrich, Germany, model PAM-2000). Protocols and parameters for fluorescence measures are given in Chapter 5. During the summer of 2000, effective quantum yield (ϕPSII) and maximum quantum yield (F_v/F_m) measurements were taken at three replicate sites for each species. Site means are from measurements on nine colonies per site. Plants were watered to ensure full photosynthetic activity and colonies were covered for at least 30 minutes by 15cm x 15cm squares of black plastic to dark adapt the plants and allow ample time for full rehydration. Measurements were taken on overcast days with lower temperatures to increase efficiency of dark adapting the plants with black plastic, and to limit immediate physiological stress during ϕPSII measurements. After F_v/F_m measurements were made on the dark-adapted plants, the colonies were watered again and covered with clear plastic pieces to maintain hydration and control for effects of covering the plants. The plants were light-adapted for at least 30 minutes before ϕPSII measurements were taken. Temperature and photosynthetic photon flux (PPF) were also recorded with each ϕPSII measurement. Because of the nature of *M. macrocarpa* cliff habitat, dark-adaptation of colonies was only possible at one of the sites. F_v/F_m measurements and ϕPSII measurements revealed similar between species differences, but because of the lack of replication for F_v/F_m measures on *M. macrocarpa* mainly yield ϕPSII measurements are presented. The congruence of F_v/F_m and ϕPSII measurements indicates that species differences were not due to differences in ambient environment conditions, but instead to more long term differences in photosynthetic efficiency relating to the photosystem machinery.

Reciprocal colony transplants.—Reciprocal transplant experiments test the long-term physiological tolerance of species to grow as colonies outside of their current habitats (e.g., Alpert 1988, Kooijman 1993, Frego & Carleton 1995) and may also reflect competitive interactions if stems are in close contact with other species (Mulligan & Gignac 2001). Two reciprocal transplant experiments were conducted: 1) colony transplants without neighbor contact to examine the effect of site environment on survival and 2) 4 cm^2 stem bundle transplants in contact with neighbors to examine the combined effect of environment and neighbors. In 1998, reciprocal adult transplants were made for each species at five native and five non-native sites. These sites were the same sites used in the establishment experiments. Transplant methodology varied somewhat by species again because of differences in substrate type. For transplanting between *M. macrocarpa* sites, adult colonies were removed from the original habitat and glued to cement discs using an inert glue (EcoFlex). Cement discs rather than rock from the sites were used to minimize disturbance to *M. macrocarpa* rock cliff habitats. For all species, colonies were maintained in a cool, dark environment (cooler and /or refrigerator) in sealed plastic bags to minimize physiological stress caused during transplantation. Transplants were made within the same day for five of the six species and within three days for all species. *Mielichhoferia macrocarpa* required more time for the glue to dry properly. All transplants were photographed at the time of transplantation and again in September 1998. Transplant sizes varied between species because of differences in plant size and rarity. *Mielichhoferia macrocarpa* had the smallest transplants (12 cm^2), *B. pseudotriquetrum*, *D. johansenii* and *D. rigidulus* transplants were medium sized (45 cm^2), and the two species of *Mnium* were largest (130 cm^2). Transplants were evaluated *in situ* in September 2000 using the same scoring system as for colony re-assessments. Most *M. macrocarpa* transplants were lost to disturbance while *B. pseudotriquetrum* transplants became indistinguishable from the surrounding colonies at their native sites. *Didymodon rigidulus* transplants were all lost to disturbance at native sites.

A second transplant experiment was set up for *M. macrocarpa*, *B. pseudotriquetrum*, *M. arizonicum* and *M. spinulosum* in spring 1999 to complement fragment neighbor experiments for these species. The experiments used smaller, $4cm^2$ stem bundle transplants that would be in closer association with the surrounding species. In June 1999, stem bundles of *M. macrocarpa*, *B. pseudotriquetrum, M. arizonicum* and *M. spinulosum* were reciprocally transplanted at the 1998 sites. The moss stems were held together by galvanized wire gently wrapped around the transplant and these stems were then placed into the middle of an existing colony. In September 2000, these transplants were scored for survival and percent of green stems when survival did not differ between species (i.e., *M. arizonicum* and *M. spinulosum*). Transplant survival was compared by Chi-square contingency for six species after three years and for four species after 15 months. *A priori* species pair comparisons for transplant survival were also made by Chi-square contingency analysis. The percent of green stems in *Mnium* neighbor contact transplants were compared by two-way ANOVA (species by site). Planned comparisons were made between the *Mnium* species and between native versus non-native transplants (Sokal & Rohlf 1981).

Colony neighbor interaction.

There have been many methods developed to study competition; however, replacement series experiments that compare the performance of a plant grown alone to its performance mixed with another species remain the most commonly employed (e.g., replacement series of De Wit (1960)). This method has been applied to upland bryophytes in forests (McAlister 1995) and grasslands (Zamfir & Goldberg 2000). However, mosses are typically slower growing than vascular plants and the length of time appropriate for competition studies in bryophytes is unclear (e.g., Rydin 1986, 1993). Here I use a method developed by Kimmerer (1994) for scoring competition in upland bryophytes without experimental manipulation.

In 2000, three restricted-random 1m wide belt transects were set-up at one site per species for all species except *M. macrocarpa*. For the first fifty colonies encountered along the transect, size of colony (length of longest axis and perpendicular to longest axis), distance along the transect and neighbor contact was recorded. If neighbor contact occurred, the target species and neighbor species colonies were dissected apart to determine whether one species had overgrown the other (win or loss) or whether both species were beginning to intermingle stems at the shared border (tie). Because *M. macrocarpa* is the rarest study species and disturbance to living colonies was undesirable, and because this species occurs on rock cliffs where it is impractical to run a transect, competition scores were obtained from tracings of three study populations. The tracings included all moss colonies on the cliffs and were taken in 1998 and again in 2000. These methods are comparable to the other five species for neighbor encounter rates, but not for contact outcome. The number of neighbor encounters and the percentage of those encounters that were losses (excluding *M. macrocarpa*) were compared by Chi-square contingency analysis followed by Tukey-type post-hoc test for proportions (Zar 1996). For all six species, colony size was compared for colonies with and without neighbors and colonies that tied or won versus lost neighbor encounters by Mann-Whitney U test.

RESULTS

Establishment ability.

Establishment ability was assessed as the number of fragments regenerating out of those planted. Low establishment could result from low fragment recovery (i.e., disturbance) or from low regeneration of the fragments that were recovered (i.e., intrinsic limitations). There were significant differences between species in establishment ability from gametophyte fragments (Figs. 6.1, 6.2). After four months, *M. macrocarpa, D. johansenii,* and *D. rigidulus* had lower establishment than the other species with which they were compared (Fig. 6.1, and Chpt. 5, Table 5.8). For *M. macrocarpa*, low establishment corresponded with lower regeneration of those recaptured than

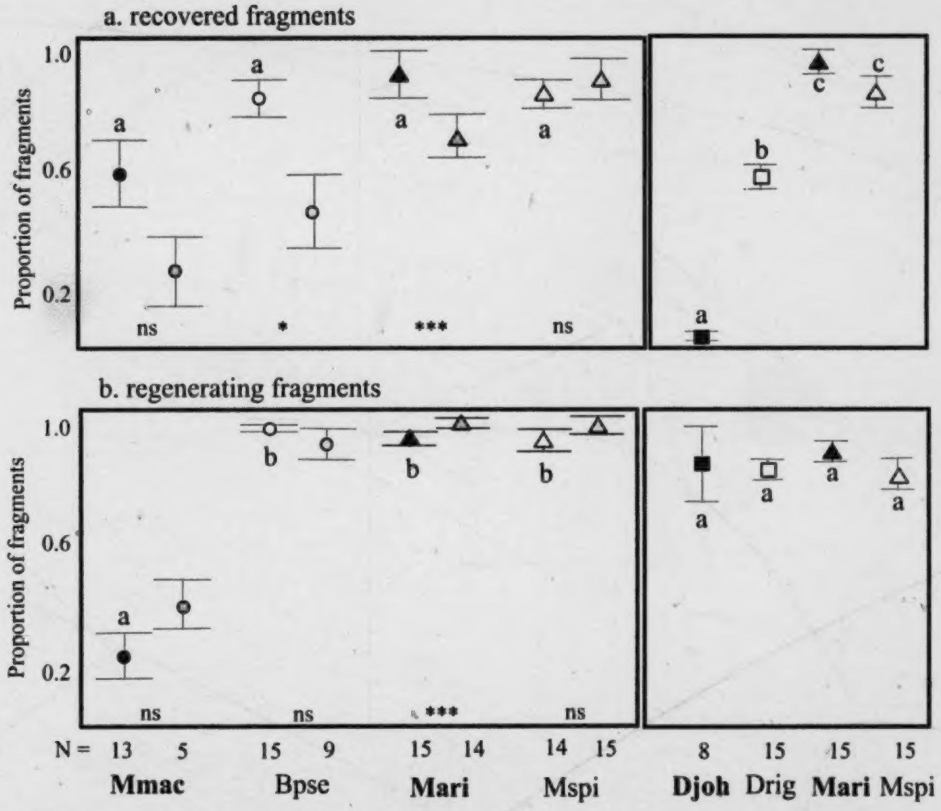

Figure 6.1. Summary of 4-month establishment plots for fragments recovered (a) and regenerating (b). *Mielichhoferia macrocarpa* (**Mmac**), *B. pseudotriquetrum* (Bpse), *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi) on the left were grown at native and non-native sites in 1998. Significance symbols above the species abbreviations denote planned comparisons on transformed data for native versus non-native fragment performance. The ANOVA analysis for each species pair is shown in Table 6.2. Native site symbols are in black (rare) and white (common) and non-native sites are in gray. On the right, *D. johansenii* (**Djoh**), *D. rigidulus* (Drig), and the two species of *Mnium* establishment in 2000 is shown. Letters associated with native site symbols separate species into post-hoc groupings from Tukey post-hoc test ($p<0.0125$) for the four species comparisons in each year. Symbols denote the mean and error bars are standard error.

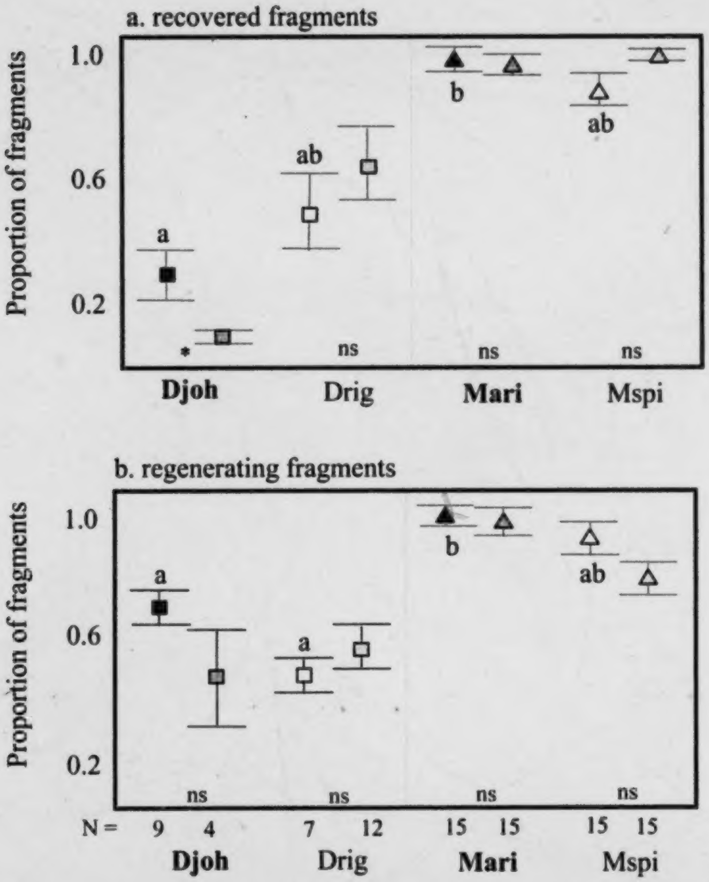

Figure 6.2. Summary of 16-month establishment plots for fragments recovered (a) and regenerating (b). *Didymodon johansenii* (**Djoh**), *D. rigidulus* (Drig), *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi) were grown at native and non-native sites from May 1999 - August 2000. Significance symbols above the species abbreviations denote planned comparison for native versus non-native fragment performance. Native site symbols are in black (rare) and white (common) and non-native sites are in gray. Letters associated with native site symbols separate species into post-hoc groupings from Tukey post-hoc test ($p<0.0125$) for the four species comparisons in each year. Symbols denote the mean and error bars are standard error.

M. arizonicum, *M. spinulosum* and *B. pseudotriquetrum* (Fig. 6.1b; $F_{3,20} = 24.327$, $p < 0.001$). For *D. johansenii*, low establishment reflected a lower proportion of recovered fragments than *D. rigidulus*, *M. arizonicum* and *M. spinulosum* (Fig. 6.1a; $F_{3,20} = 10.161$, $p < 0.01$). *Didymodon rigidulus* had lower fragment recovery than *M. arizonicum* and *M. spinulosum* (Fig. 6.1a). In 1998 and 2000, the two species of *Mnium* consistently had the highest relative establishment ability (Fig. 6.1, Chpt.5, Table 5.8).

In the comparisons of establishment at native and non-native sites, species varied in their responses (Table 6.2, Figs. 6.1 & 6.2). Note that the non-native sites of the rare species are the native sites for the common species for all species pairs in Figures 6.1 and 6.2. Only *D. johansenii* had significantly lower establishment at non-native sites because of significantly lower fragment recovery (Fig. 6.2), which accounted for the significant species by site interaction for fragment recovery (Table 6.2). In 1998, *B. pseudotriquetrum* and *M. arizonicum* also had lower fragment recovery at non-native sites, but this was balanced by high regeneration and did not result in lower overall establishment (Fig. 6.1). *Mielichhoferia macrocarpa* and *B. pseudotriquetrum* had a site by species interaction for fragment regeneration (Table 6.2) explained by higher fragment recovery of *B. pseudotriquetrum*, but not *M. macrocarpa* at *B. pseudotriquetrum* sites (Fig. 6.1).

In *Mnium* plots that were in the field for 16 months, *M. arizonicum* had higher establishment from gametophyte fragments than *M. spinulosum* (Table 6.3, Fig. 6.3). No effect of site or neighbor presence on fragment recovery was detected (Table 6.3). Species regeneration varied by site (Table 6.3) primarily due to lower regeneration at *M. arizonicum* sites in all but the *M. arizonicum* alone treatment at those sites (Fig. 6.3b). For the putative *Bryum* congeners, *M. macrocarpa* had lower establishment (69%±37) than *B. pseudotriquetrum* (84%±27) after 4 months (Table 6.4). Both species had lower regeneration where plot disturbance was high at *M. macrocarpa* site 3 (*M. macrocarpa*, 15%±21 and *B. pseudotriquetrum*, 44%±29) and site 2 (*M. macrocarpa*, 48%±40 and *B. pseudotriquetrum*, 73%±37), although site 2 did not differ from site 5 (Tukey HSD post-hoc, $\alpha = 0.05$). No effect of neighbor presence on establishment of these two species at *M. macrocarpa* sites was detected (Table 6.4).

Table 6.2. Effect of species and site on fragment regeneration and recapture. Two-way ANOVAs by species pair on the proportion of fragments alive out of those planted and the number of fragments found out of those planted (for all balanced models df = 60). Actual data is shown in Figure 6.1. Variation in degrees of freedom reflects unbalanced models resulting from plot disturbance. Significance of F-values, ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and for values close to $p = 0.05$ the actual p-value is given as a superscript. Significant site by species interactions may represent the effect of native versus non-native sites on establishment and this *a priori* hypothesis was explored using planned comparisons (see text).

Species pair (year - duration)	Source	df	MS_{regen}	F_{regen}	df	$MS_{recover}$	$F_{recover}$
Mmac - Bpse (1998 - 4 mos)	Species	1	6.328	80.79***	1	1.450	$3.855^{0.057}$
	Site	9	0.057	0.725^{ns}	9	0.226	0.619^{ns}
	Species * site	7	0.230	2.932*	9	0.771	$2.116^{0.051}$
Mari - Mspi (1998 – 4 mos)	Species	1	0.004	0.113^{ns}	1	0.037	0.266^{ns}
	Site	9	0.054	1.409^{ns}	9	0.222	1.577^{ns}
	Species * site	9	0.039	1.937^{ns}	9	0.0944	0.670^{ns}
Djoh - Drig (2000 – 16 mos)	Species	1	0.001	0.012^{ns}	1	4.491	20.68***
	Site	8	0.103	$2.633^{0.047}$	9	0.543	2.500*
	Species * site	6	0.081	2.081^{ns}	9	0.603	2.778*

Table 6.3. ANOVA analysis of fragment regeneration for two species of *Mnium* at native and non-native sites when grown in plots alone and with the species pair as neighbor from May 1999 – August 2000. Significance of F-values: ns, $p > 0.05$, *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. Model df = 120 with 1 df for model intercept in GLM.

Source	df	MS$_{regen}$	F$_{regen}$	MS$_{recover}$	F$_{recover}$
Species	1	1.342	21.47***	0.320	5.854*
Site	9	0.229	3.655***	0.082	1.500^{ns}
Neighbors	1	0.007	0.106^{ns}	0.010	0.182^{ns}
Species * site	9	0.078	1.252^{ns}	0.042	0.764^{ns}
Species * neighbors	1	0.000	0.001^{ns}	0.002	0.034^{ns}
Neighbors * site	9	0.095	1.527^{ns}	0.080	1.454^{ns}
Species *site * neighbors	9	0.063	1.017^{ns}	0.094	1.720^{ns}
Error	80	0.062		0.055	

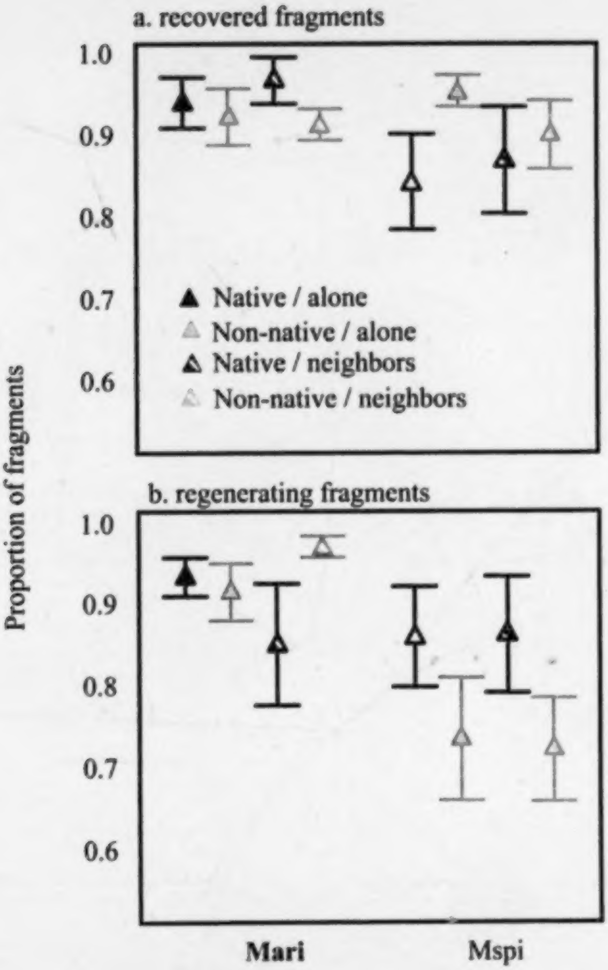

Figure 6.3. Comparison of establishment ability for two species of *Mnium*, *M. arizonicum* (**Mari**) and *M. spinulosum* (Mspi) at native and non-native sites when planted alone and with neighbors. The effects of treatment on establishment are separated by fragment recovery (a) and fragment regeneration (b). Symbols denote the mean and error bars are standard error.

Table 6.4. ANOVA of fragment regeneration for *M. macrocarpa* and *B. pseudotriquetrum* in 1999 at *M. macrocarpa* sites after four months growing alone versus mixed together. Significance of F-values, ns, not significant, * < 0.05, ** < 0.01, *** < 0.001. Tukey HSD post-hoc multiple comparison test ($\alpha = 0.05$) was used to determine mean separation of sites.

Source	df	MS	F
Species	1	0.960	9.382**
Site	5	1.767	17.27***
Neighbors	1	0.089	0.870^{ns}
Species * site	5	0.086	0.836^{ns}
Species * neighbors	1	0.025	0.243^{ns}
Site * neighbors	5	0.161	1.578^{ns}
Site * species * neighbors	5	0.148	1.444^{ns}

Colony growth and transplantation effects.

There were significant differences between the proportion of colonies that had expanded over three years for the five study species (Fig. 6.4; $\chi^2 = 59.66$, df = 4, $p < 0.001$). *Mielichhoferia macrocarpa* had a higher percentage of expanded colonies than *B. pseudotriquetrum* and *D. johansenii* (Fig. 6.4). The two species of *Mnium* had a higher percentage of expanded colonies than *B. pseudotriquetrum* (Fig. 6.4). Only *M. macrocarpa* had higher frequency of colony expansion than its species pair (Fig. 6.4). Due to loss of mapped colonies for *D. rigidulus*, colony scores had to be taken after only one year (Fig. 6.4). Species differences for short-term *in situ* ϕPSII (Fig. 6.5; $F_{5,18} = 7.570$, df = 5, $p = 0.001$) were positively correlated to colony expansion (Pearson's $r = 0.836$, $n = 6$, $p = 0.036$). Rare species had higher ϕPSII measures than common species (planned comparison, $F_s = 71.396$, df = 1, 30, $p < 0.001$). *Mielichhoferia macrocarpa* had significantly higher yield than *B. pseudotriquetrum* and *D. rigidulus* (Fig. 6.5). Although ϕPSII differences for *in situ* colonies did not differ significantly between *D. johansenii* and *D. rigidulus*, corresponding F_v/F_m values did because of lower variation in the data (Tukey Post Hoc $p < 0.001$, data not shown).

The effect of colony transplantation to native and non-native sites on colony survival differed between species ($\chi^2 = 58.79$, df = 5, $p < 0.001$) (Table 6.5). However, *Didymodon johansenii* and *B. pseudotriquetrum* transplant survival was significantly higher at native sites for three-year colony transplants (Table 6.5a). *Didymodon johansenii* transplants had higher survival at *D. johansenii* sites than *D. rigidulus* transplants (Table 6.5b). *Bryum pseudotriquetrum* transplants had higher survival than *M. macrocarpa* at both *M. macrocarpa* and *B. pseudotriquetrum* sites (Table 6.5b). *Didymodon rigidulus* had too many transplants lost at native sites to compare with survival at *D. johansenii* sites. The two species of *Mnium* had identical transplant survival with one transplant lost for the three-year colony transplants and no losses for the 15-month transplants. After 15 months surrounded by neighbor stems, there was also no effect of site or neighbor identity on transplant survival for *M. macrocarpa* and *B. pseudotriquetrum* (Table 6.5a). Because there were no differences in overall transplant survival, the *Mnium* pair was compared by % survival of individual shoots within the

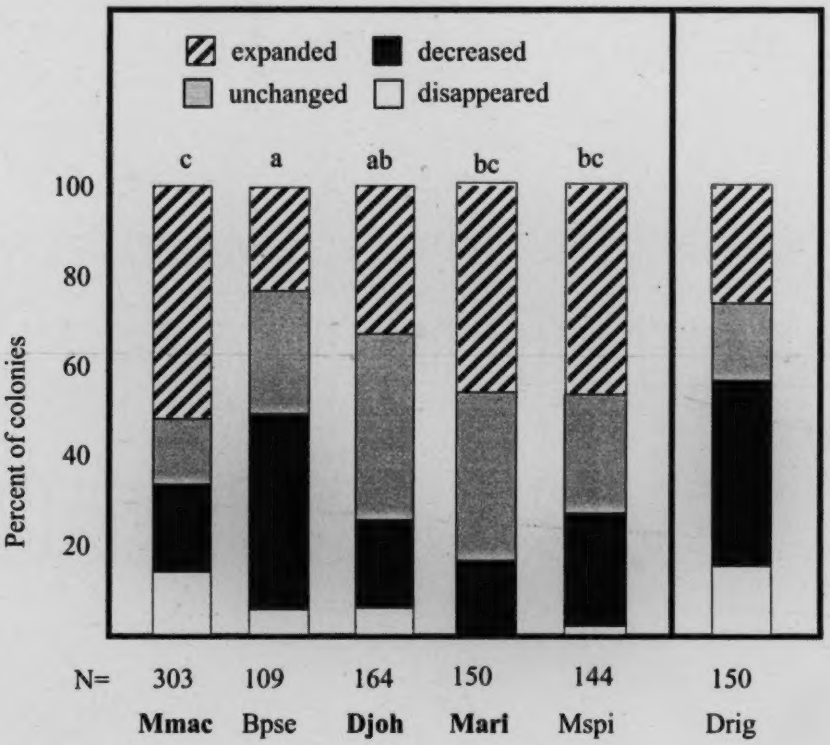

Figure 6.4. Comparison of colony expansion over three years showing the cumulative percent of colonies that expanded in size (stripes), remained the same size (gray), decreased in size (black), and disappeared (white) for five species of moss. Similar colony data for *D. rigidulus* was only obtainable after one year due to complete loss of mapped colonies after three years. Letters denote significant post-hoc differences between proportion of colonies that expanded between species.

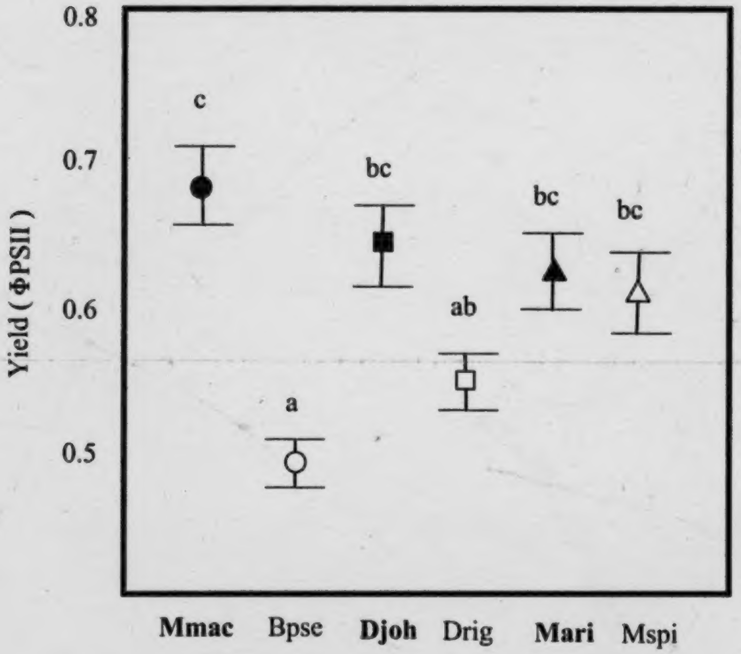

Figure 6.5. Mean separation for *in situ* yield measurements taken on six species. Means with different letters were significantly different by Tukey HSD ($\alpha = 0.05$). *M. macrocarpa* (**Mmac, ●**), *B. pseudotriquetrum* (Bpse,○), *D. johansenii* (**Djoh, ■**), *D. rigidulus* (Drig,□), *M. arizonicum* (**Mari,▲**), and *M. spinulosum* (Mspi,△). Symbols denote the mean and error bars are standard error.

Table 6.5. Chi-square analysis on counts of transplant survival for *M. macrocarpa*, *B. pseudotriquetrum*, *D. johansenii* and *D. rigidulus*.

a. Species by location at native versus pair habitat environment.

Species	Type-Year-Duration	df	χ^2	Higher survival at:
Djoh	Colony-1998-3yr	1	10.90***	**Djoh** sites
Mmac	Colony-1998-15 mo	1	3.39^{ns}	
Mmac	Bundle-1999-15 mo	1	1.00^{ns}	
Bpse	Colony-1998-3yr	1	6.53*	Bpse sites
Bpse	Bundle-1999-15 mo	1	0.18^{ns}	

b. Species pairs separated by location. Significance of chi-square values, ns, $p > 0.05$, *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. *Didymodon rigidulus* control transplants were all lost or unidentifiable and *Mnium* species had identical survival for both three-year and 15-month transplants. "Colony" transplants were whole isolated colonies, while stem "bundle" transplants were $4cm^2$ groups of stems taken from their original colonies and placed into a foreign colony (see methods for more detail).

Species pair	Sites	Type-Year-Duration	df	χ^2	Species with higher survival
Mmac-Bpse	**Mmac**	Bundle-1999-15 mo	1	6.64*	Bpse
Mmac-Bpse	Bpse	Bundle-1999-15 mo	1	8.57**	Bpse
Djoh-Drig	**Djoh**	Colony-1998-3yr	1	10.90***	**Djoh**

transplants after 15 months in the field (Fig. 6.6). The two species of *Mnium* responded differently to the sites (df = 9, $F_{20,40} = 2.198$, p = 0.043), and both site (df = 9, $F_{20,40} = 2.406$, p = 0.028) and species (df = 1, $F_{20,40} = 22.80$, $p < 0.001$) affected the percent of green shoots in the transplants (Fig. 6.6). *Mnium arizonicum* had a higher percentage of green shoots at *M. spinulosum* sites (Fig. 6.6; planned comparison, $F_s = 5.879$, df = 1, 21, $p < 0.05$). *Mnium spinulosum* did not differ in transplant health between native and non-native sites (Fig. 6.6; planned comparison, $F_s = 0.507$, df = 1, 21, $p > 0.05$). *Mnium arizonicum* had a higher mean percentage of green shoots in all transplants than *M. spinulosum* (Fig. 6.6; planned comparison, $F_s = 11.41$, df = 1, 59, $p < 0.05$).

Colony disappearance and neighbor contact.

After three years, there were significant between species differences in colony disappearance (Fig. 6.7; $\chi^2 = 688$, df = 5, $p < 0.001$). *Mnium arizonicum* had the lowest colony disappearance of all species except *M. spinulosum* (Fig. 6.7). The low disappearance of adult colonies at *Mnium* sites agrees with the high recovery of fragments at these sites (Figs. 6.1-3). However, the relationship between fragment disappearance over 4 months and colony disappearance over three years was not significant for all six species (Pearson's r = 0.138, df = 5, p = 0.794). In contrast to *M. arizonicum*, *D. rigidulus* had 100% of colonies disappeared after three years (Fig. 6.7). Observations on additional mapped colonies found that 62 out of 150 colonies disappeared in 4 months. *Didymodon rigidulus* was the only species with significantly greater colony disappearance than its species pair (Fig. 6.7).

There was no linear relationship between the percent of colonies disappeared and the percent of colonies with neighbor encounters (Pearson's r = -0.683, n = 6, p = 0.135). Frequency of neighbor encounters (Fig. 6.8, inset; $\chi^2 = 293$, df = 5, $p < 0.001$) and the relative frequency of encounter outcomes (Fig. 6.8; $\chi^2 = 85.7$, df = 4, $p < 0.001$) differed between the species that were comparable. *Didymodon johansenii*, *D. rigidulus*, and *M. macrocarpa* had the lowest frequency of neighbor contact (Fig. 6.8, inset). *Mielichhoferia macrocarpa* had lower frequency of neighbor contact than *B. pseudotriquetrum*, and the other two species pairs did not differ in frequency of neighbor

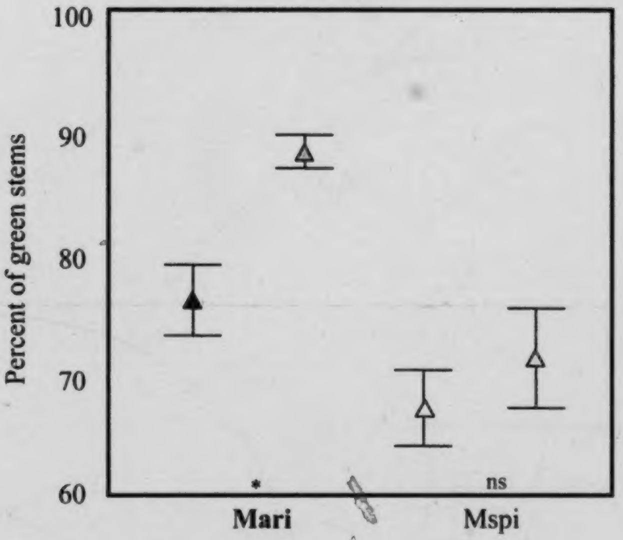

Figure 6.6. Comparison of percentage of green stems in four-month reciprocal transplants of stem bundles into neighbors at native (black and white triangles) and non-native (gray triangles) sites for *M. arizonicum* (**Mari**) and *M. spinulosum* (Mspi). Significance symbols are for planned comparisons of performance at native versus non-native sites: ns, $p > 0.05$, * $p < 0.05$. Symbols denote the mean and error bars are standard error.

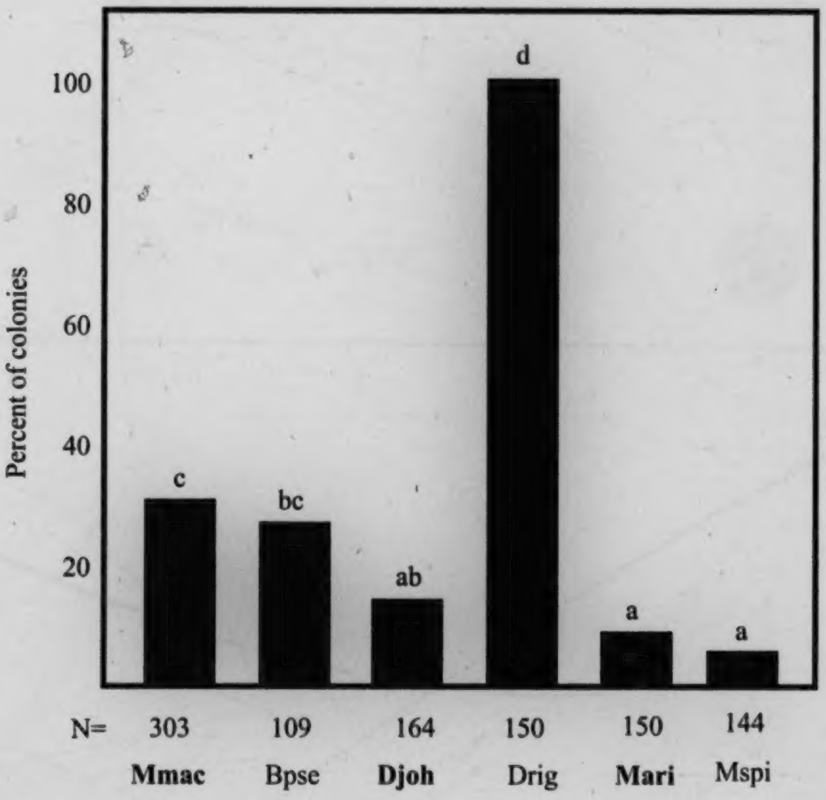

Figure 6.7. Percent of colonies that had disappeared after three years for six mosses, *M. macrocarpa* (**Mmac**), *B. pseudotriquetrum* (Bpse), *D. johansenii* (**Djoh**), *D. rigidulus* (**Drig**), *M. arizonicum* (**Mari**), and *M. spinulosum* (Mspi). Letters above the bars show percentages that differed between species for disappeared colonies in Tukey-type post hoc comparison ($\alpha = 0.05$).

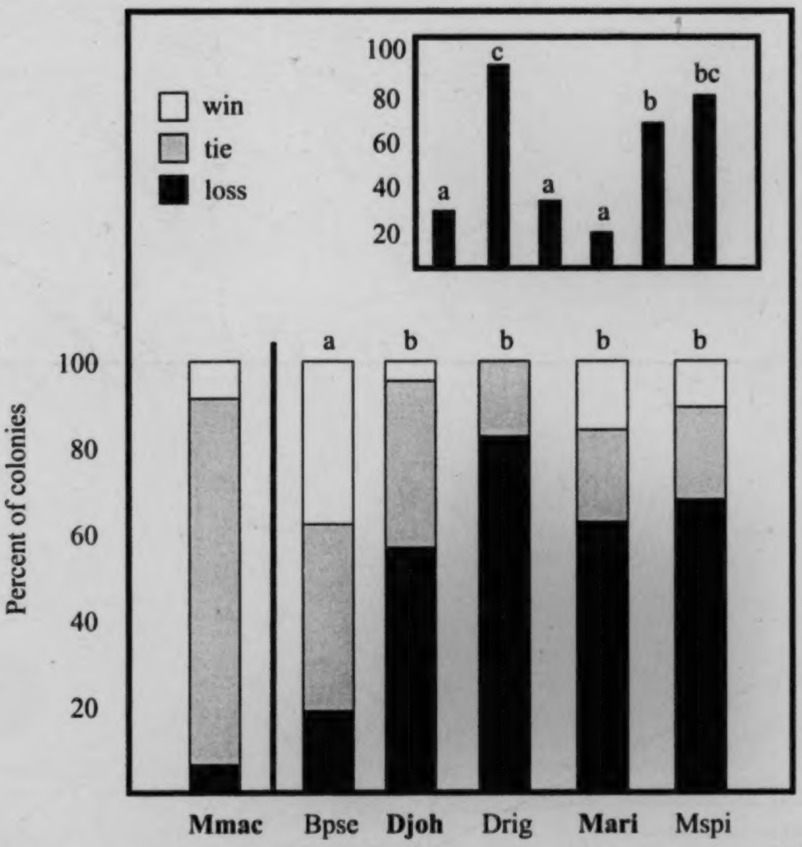

Figure 6.8. Between species differences in frequency of neighbor encounter(inset) and relative percent of encounter outcomes. In the inset, post-hoc differences in percentage of neighbor encounters are shown by letters above the bars. Species with different letters are different by Tukey-type test for proportions ($\alpha = 0.01$). Encounter outcomes are win (white bar), tie (gray bar) and loss (black bar). Species are abbreviated by the first letter of their genus and first three letters of their specific epithet. M. macrocarpa was not included in the comparison of losses because of methodological differences (see text for details). The letters denote species with different percentage of losses (Tukey-type test for proportions, $\alpha = 0.01$).

encounters (Fig. 6.8, inset). Between species, the frequency of neighbor contact was positively correlated with the percentage of outcomes won (Pearson's $r = 0.831$, $n = 6$, $p = 0.040$). *Bryum pseudotriquetrum* lost a lower percentage of neighbor encounters than the other four species (Fig. 6.8). None of the species pairs differed in the frequency of encounter losses (Fig. 6.8). *Mielichhoferia macrocarpa* colonies were difficult to score and most of the encounters appeared to be ties (Fig 6.8) likely because of the short time period (two years) involved. Within species, larger colonies had greater frequency of neighbor contact for all species, although note *M. arizonicum* has $p > 0.05$ (Table 6.6a). Larger colonies were not less likely to lose in encounters for any of the species (Table 6.6b).

DISCUSSION

Comparison of species limitations.

By including rare-common species pairs, establishment and adult limitations, and abiotic and biotic restrictions, this study encompasses many levels of comparison. The clearest difference between rare and common species was the higher *in situ* yield of rare species (Fig. 6.5). Establishment limitations were more important than colony limitations for two of the three rare species, *M. macrocarpa* and *D. johansenii*. Establishment limitations observed here agree with prior experiments (Chpts. 3 & 4) that substrate is the most critical abiotic factor for *M. macrocarpa* and disturbance regime is the most critical factor for *D. johansenii*. Biotic restrictions were not detected for any of the species as fragments or colonies. Within pair differences between rare and common species in this study may reflect differential influence of establishment, competition and disturbance on local persistence of the species.

The main differences between *M. macrocarpa* and *B. pseudotriquetrum* were the consistently lower regeneration of *M. macrocarpa* in all establishment experiments and the higher *in situ* yield and colony expansion of *M. macrocarpa* at its native sites where colony encounters are lower than in *B. pseudotriquetrum* sites. These two species did not differ in colony disturbance. Both species appear to be relatively strong competitors in

Table 6.6. Colony size differences by frequency of neighbor encounters and outcome of neighbor encounters.

a. Mann-Whitney U comparing colony sizes by encounter occurrence for each species.

	Encounter		No encounter			
Species	N	mean (sd) cm^2	N	mean (sd) cm^2	Z	p
Mmac	64	25.84 (27.05)	198	20.10 (26.56)	-2.041	0.041
Bpse	132	778.1 (5414)	18	41.53 (66.63)	-2.314	0.021
Djoh	44	18.32 (31.56)	107	5.70 (7.35)	-3.181	0.001
Drig	23	29.82 (73.68)	127	2.01 (3.88)	-4.747	<0.001
Mari	94	86.38 (108.9)	56	53.46 (71.03)	-1.834	0.067
Mspi	112	69.15 (83.79)	38	28.89 (54.17)	-4.166	<0.001

b. Mann-Whitney U comparing colony sizes by encounter outcome for the six species.

	Tie or win		Loss			
Species	N	mean (sd) cm^2	N	mean (sd) cm^2	Z	p
Mmac	44	28.03 (29.73)	5	18.1 (15.53)	-0.694	0.510
Bpse	106	799.7 (5853)	26	685.8 (3116)	-0.080	0.936
Djoh	20	14.02 (17.09)	24	21.91 (39.89)	-0.059	0.953
Drig	4	13.38 (15.22)	19	33.28 (80.77)	-0.082	0.969
Mari	37	87.46 (105.2)	58	84.41 (111.5)	-0.130	0.897
Mspi	38	59.69 (70.79)	74	74.01 (89.80)	-0.621	0.535

their native sites compared to the other four study species (Fig. 6.8). However, relative to *B. pseudotriquetrum*, *M. macrocarpa*'s low establishment and lower transplant survival suggests this species may only be able to establish in sites not currently occupied by other mosses, after which it rapidly expands through clonal propagation. *Mielichhoferia macrocarpa* is restricted to calcareous substrates during establishment (Cleavitt 2001, Chpt.3), and lack of site effect here likely resulted because substrate was held constant (i.e., all sites had cement disks, Table 6.1). This hypothesis was supported in 1999 when *M. macrocarpa* was planted on soil screen plots at the five *B. pseudotriquetrum* sites using soil from those sites and none of the *M. macrocarpa* fragments established (unpub. data). The higher overall survival of *B. pseudotriquetrum* transplants compared to *M. macrocarpa* in conjunction with the higher survival of three-year transplants at native sites suggests that *B. pseudotriquetrum* is occupying sites where it can grow best despite low *in situ* yield (ΦPSII). The high number of neighbor encounters and low number of encounter losses indicate the ability of *B. pseudotriquetrum* to compete for these sites. *Mielichhoferia macrocarpa* had fewer neighbor encounters than *B. pseudotriquetrum* and despite the relatively low number of encounter losses, competition may play a relatively small role in *M. macrocarpa*'s persistence at a site. Independent evidence of low neighbor density at *M. macrocarpa* sites was gained in survey comparisons between three *M. macrocarpa* sites and three sites that seemed suitable but had no *M. macrocarpa* colonies. Sites with *M. macrocarpa* had a higher percentage of bare rock (73%±28) than sites without *M. macrocarpa* (17%±22) (unpub. data). Continued exploration into ecological limitations of *M. macrocarpa* should include the relative effects of environmental parameters and neighbors on the rates of establishment from gametophyte fragments and spores and subsequent colony expansion.

Both *D. johansenii* and *D. rigidulus* were able to survive as colonies and fragments in one another's habitats, and both appear more influenced by disturbance than competition. The primary limitation for *D. johansenii* is during the establishment stage due to the disturbance regime (Chpt. 4). Although fragment recovery is low at native sites, it becomes even lower at *D. rigidulus* sites (Fig. 6.2). *Didymodon johansenii*, had higher *in situ* yield (F_v/F_m) than *D. rigidulus* and higher transplant survival at native sites where it survives better than *D. rigidulus*. Death of *D. rigidulus* transplants at *D. johansenii* sites was due to burial by spruce needle litter rather than sub-optimal environmental conditions, as evidence by luxuriant growth and the only observed sporophyte production by *D. rigidulus* during the study. These two species occur in habitats with relatively low neighbor contact (Fig. 6.8, inset), high disturbance during establishment (Figs. 6.1 & 6.2), and appear restricted to microsites with low neighbor density. *Didymodon johansenii* and *D. rigidulus* may be more successful at establishing in previously unoccupied sites than neighboring species because of higher desiccation tolerance (Chpt. 5), i.e., they are stress tolerators. An experiment comparing the relative establishment ability of these *Didymodon*s with co-occurring species would help to determine whether they are limited to previously unoccupied habitats during the establishment stage.

Mnium arizonicum was the only rare species that may have both higher establishment and competitive ability than its common species partner; however, these greater abilities were not restricted to *M. arizonicum* sites. In fact, *M. arizonicum* had higher regeneration and transplant health after 15 months at *M. spinulosum* sites. This pattern is consistent with those shown for invasive species, i.e., species capable of expanding their range (Richardson & Bond 1991, Grigulis *et al.* 2001). Unlike *M. macrocarpa* and *D. johansenii*, *M. arizonicum* exhibited the potential to expand into non-native sites, i.e., outside its realized niche. The major ecological difference between *M. arizonicum* and *M. spinulosum,* which may explain their distribution differences, is the extremely rare sporophyte production in *M. arizonicum* contrasted with prolific sporophyte production in *M. spinulosum* (Chpts. 2 & 5). For this species pair dispersal limitation seems the most likely explanation of *M. arizonicum*'s rarity.

Based on differences in the rare species' current distribution patterns and biogeography, differences between limitations of the rare species were not wholly unexpected. *Mielichhoferia macrocarpa* and *D. johansenii* share similar geographic distributions and both were hypothesized to belong to an ancient, once widespread flora that survived glaciation in refugia such as Beringia (Steere 1978). These two rare species are likely relatively old species adapted to habitats that have become patchily distributed on the landscape. This hypothesis would gain support from experiments that demonstrate that these species occur in habitats that represent their physiological optimum (e.g., the relatively high *in situ* ΦPSII demonstrated here), and that in these habitats they can out-compete other species. In contrast, the North American endemic species, *M. arizonicum*, may conform to the metapopulation theory of Hanski (1991) which predicts poor dispersal and low population growth rates for rare species. *Mnium arizonicum* relies almost entirely on asexual reproduction and the only sporophytes observed over four years were consumed by an unidentified herbivore. Therefore, the most likely limitation for *M. arizonicum* is poor dispersal ability as there were no detectable limitations to its local persistence.

Comparison to existing hypotheses.

The idea that common species live in more widespread habitats and rare species live in more restricted habitats (Prober & Austin 1990, Hanski *et al.* 1993) is supported by these three species pairs (Table 6.7, Chpt. 2, 3). In this study and in Chapter 5 this pattern was related to differences in the relationship of species' fundamental and realized niches. Brown's (1995) niche-based hypothesis predicts niche relationship differences between rare and common species, and suggests that rare species have narrower realized niches because they have smaller fundamental niches than common species. This was found only in the regeneration niche for two of the three rare species here (Table 6.7). Species with large fundamental niches relative to their realized niches should be poor competitors and species whose fundamental and realized niches are similar should be strong competitors (Hutchinson 1957 as elaborated by Keddy 1989). The pattern of rare species with a wide fundamental niche and narrow realized niche has been found in several studies including aquatics (Greulich *et al.* 2000), shrubs (Witkowski & Lamont 1997), and trees (Prober 1992). In this study, two of the rare species, *M. macrocarpa* and *D. johansenii*, were restricted by habitat related establishment requirements and the third species, *M. arizonicum*, had no discernable proximal reason for habitat restriction. The three common species have physiological limitations in the establishment (Chpt. 3) and

Table 6.7. Summary of experimental results from this study with relation to relevant theory predictions. Symbols in support column are: ±, conflicting results, +, weak support, ++ support.

Topic: Source	Prediction	Support	Comments from results
Rarity theory: Prober & Austin 1990	Rare species are restricted to rare habitats	+	Mmac had lower survival of 15-month transplants at Bpse sites. Habitat rarity not assessed directly. No difference in establishment at native versus non-native sites.
Hanski *et al.* 1993	Rare species use rare (abiotic) resources	++	Abiotic restrictions of Mmac & Djoh (see also Chpts 3 & 4). Resource rarity not assessed directly. No difference in establishment at native versus non-native sites or in presence of neighbors.
Holt *et al.* 1997	Rare species have lower establishment ability and lower growth rates	±	Mmac & Djoh have lower establishment, but all rare species had higher growth rates.
O'Connor 1987	Rare species have higher growth rates or lower neighbor contact at native sites and lowered performance in presence of neighbors at non-native sites.	±	Rare species all had higher growth rates at their native sites in comparison with common species, but there was no difference in performance in the presence of neighbors in establishment or colony stage. Neighbor encounters were lower for Mmac relative to Bpse.
Brown 1995	Rare species have narrower fundamental niches	+	In the regeneration niche of Mmac and Djoh. However, there was no difference in survival of reciprocal transplants for rare species. Also see Chapter 5.
Krukeberg 1951, Robson & Maze 1995	Physiological restrictions of rare species are imposed by neighbor interactions	+	Djoh and Mmac both grow in habitats with few neighbor encounters. All rare species are capable of surviving beyond their current habitat. Neighbor interactions did not influence survival.
Plant strategy theory: Harper *et al.* 1961, Grubb 1977	Species distributions reflect establishment limitations	++	Djoh had higher establishment at native sites. When Mmac grown on Bpse soil, there was no establishment (see Discussion text).
Grime 1979	Neighbor interaction lower in habitats with higher colony disturbance	+	Not a linear relationship, but species with lowest neighbor contact had highest disturbance, Drig, and visa versa for Mari and Mspi.

adult stages (Chpt. 5). Therefore, *M. arizonicum* is the species most likely to have a broader fundamental than realized niche. However, determination of fundamental and realized niche relationships would require evidence of competitive exclusion, which was not documented in this study.

Lower establishment in two of the three rare species lends limited support to the "vital rates" hypothesis (Table 6.7), which has also been supported by demographic comparisons of rare and common vascular species (Morley 1982, Rabinowitz *et al.* 1989, Byers & Meagher 1997, Fiedler *et al.* 1998). Contrary to predictions of O'Connor (1987), the presence of neighbor fragments did not affect the establishment of *M. macrocarpa*, *B. pseudotriquetrum*, *M. arizonicum* or *M. spinulosum*, and the distribution patterns of these species appear not to have resulted from competitive interactions in the establishment stage. The lack of competitive interactions in the establishment stage coincides with the lack of neighbor effect for these species in the colony stage (i.e., 15-month reciprocal bundle transplants; Table 6.8), and agrees with findings of no competitive interactions between bryophytes in other upland bryophyte systems (see review by Slack 1990). Gametophyte fragments may be less susceptible to chemical inhibitory effects than spores (Miles & Longton 1990, Longton 1994, 1997) and species may be less inhibited by co-establishing propagules than by pre-established colonies (Watson 1981, Newton & Mishler 1994). Vascular plant establishment studies with neighbors concluded that in short-term time scales involved in many investigations of competition neighbor presence affects growth, but not survival (Howard & Goldberg 2001, Peltzer & Wilson 2001). Future establishment experiments on bryophyte competition should evaluate differences in growth of fragments.

There was evidence of higher growth rates (i.e., higher *in situ* yield and/or colony expansion) of all three of the rare species' colonies relative to their common partners which contradicts the predictions of O'Connor (1987) and Holt *et al.* (1997) for rare species (Table 6.7). Inferred higher relative growth rates of *M. macrocarpa* and *D. johansenii* may partly be a reflection of lower physiological stress in the habitats where they occur relative to their common pair (Chpt. 5). For *M. arizonicum*, higher colony performance may reflect greater stress tolerance in comparison with *M. spinulosum*

(Chpt. 5). Overall, ability to win or tie in a neighbor interaction appeared to vary along phylogenetic rather than rarity lines with only the putative congeners *M. macrocarpa* and *B. pseudotriquetrum* having fewer encounter losses than the other four species (Fig. 6.8).

There was weak support for the "plant strategy theory" prediction that habitats with lower disturbance would have greater competition, since habitats with a lower percent of colonies disappearing also experienced a higher percentage of neighbor interactions (Table 6.7, Figs. 6.7, 6.8). This is the first comparison between the frequency of neighbor interaction and the frequency of disturbance in bryophytes occurring in habitats with different disturbance regimes. Further exploration of this relationship would help to clarify whether disturbance regime differences can explain documented differences in the importance of competition for bryophytes in more stable habitats, such as peatlands, versus less stable upland systems studied here (Slack 1990). Documentation of colony disappearance is also important for metapopulation models where extinction rate in a patch is an important parameter (Söderström & Herben 1997), and Söderström & Herben (1997) cite Jonsson and Söderström (1988) as the only study documenting colony extinction for bryophytes. Jonsson and Söderström (1988) report 1 out of 50 marked colonies of the liverwort, *Ptillidium pulcherrimum,* disappeared over four years, which is a much lower extinction rate than the mosses in this study (Fig. 6.7). In this study, there was some indication that species may be better adapted to the disturbance regimes in their native habitats, as *D. johansenii*, *M. arizonicum* and *B. pseudotriquetrum* all had significantly lower fragment recovery at non-native sites (Figs. 6.1 & 6.2). In contrast to the results of many vascular plant studies, which have demonstrated the importance of disturbance regime to rare species (e.g., McIntyre 1995, Allphin & Harper 1997, Hamzé & Jolls 2000, see Chpt. 1 and Appendix A), disturbance regime only limited one of the three rare species in this study, *D. johansenii*.

Conclusion.

The rare species here appear to have higher *in situ* yield (ΦPSII) in their native habitats than the common species do in their respective habitats, and these inferred higher growth rates suggest that the rare species are not occupying sub-optimal sites from a physiological viewpoint. Local persistence of two of the three rare species was limited during the establishment stage by physiological and physical abiotic factors. One of the common species, *D. rigidulus*, was limited by high disturbance at both the establishment and colony stages. The limitations of the other two common species were found to relate to physiological limitations (Chpt. 5) not exceeded by the transplant sites used here. The third rare species, *M. arizonicum*, appears limited in its ability to disperse rather than its ability to persist.

In terms of current rarity hypotheses, Hanski *et al.* (1993) and Brown (1995) received the strongest support from this study. None of the hypotheses were completely at odds with results presented here; however, conflicting results were obtained in reference to predictions of O'Connor (1987) and Holt *et al.* (1997). Importance of the establishment stage in local persistence of three of the six species here supports the theories of Harper *et al.* (1961) and Grubb (1977). Future experiments examining competition of bryophytes in the regeneration niche should attempt to distinguish between results caused by differential establishment abilities and effects of chemical inhibition. The division of establishment ability into physical and physiological components can distinguish between two functionally different causes of low establishment, attachment and regeneration, and should also further our understanding of interactions during establishment (e.g., Kennedy & Bruno 2000).

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Chapter 7: Synthesis: does the autecology of six moss species reflect rarity or phylogeny?

Previous attempts to detect ecological or life history traits associated with rarity have synthesized information from surveys, descriptive floras and field guides (e.g., Hodgson 1986, Rabinowitz *et al.* 1986, Lahti *et al.* 1991, Gustafsson 1994, Médail & Verlaque 1997, Thompson *et al.* 1998, Hedge & Ellstrand 1999, Pyron 1999, Yu & Dobson 2000). Such an approach allows the inclusion of more species than one based on autecological studies. However, the trait associations identified from surveys do not necessarily define functional relationships (Hedge & Ellstrand 1999). For instance, the most common relationship considered in such studies was geographical range and habitat specificity or breadth (Thomas & Mallorie 1985, Hodgson 1986, Rabinowitz *et al.* 1986, Arita *et al.* 1990, Yu & Dobson 2000). Yet in this thesis, I have demonstrated that reported habitat specificity of a species can result from many different mechanisms (Chpts. 3, 4 & 6).

Empirical studies have thus far been of limited use for trait comparisons because the limited number of species compared in these studies. Of 149 empirical ecological studies on rare plant species that I have reviewed, 128 have focused on only rare species, and the 21 comparative studies often include a single species pair (Appendix A). Four of the comparative studies with congeneric pairs have included more than a single pair (Fiedler 1987, Karron 1987, Robson & Maze 1995, Fiedler *et al.* 1998), and of these only Karron (1987) included two complete pairs (i.e., two rare and two common species) both from the same genus, *Astragalus* (Appendix A). Baskin *et al.* 1997 presented a review of work on three Tennessee cedar glade endemics and their common congeners; however, they summarize three separate sets of data or "case studies". The works of Karron (1987) and Baskin *et al.* (1997) lack the ability to generalize for other rare-common species pairs. The former because conclusions are based on a single plant genus and the latter for its focus on a single type of rare species. The series of studies analysed here represents a unique data set that includes three rare-common plant species pairs representing three separate genera. The study also includes several rarity categories (*sensu* Rabinowitz

1981, see Chpt. 2). Patterns consistent between rare-common species pairs from three genera should be more generalizable or at least form a more sound line of evidence by which to formulate new rarity hypotheses.

With this data set, I pose two main questions: 1) do ecological similarities between my species reflect phylogeny or rarity (Fig. 7.1)? 2) Do any ecological traits tend to co-occur, and if so, are different trait patterns found among rare or common species? Ecological similarity of the six moss species is explored using cluster analysis to determine which species are most similar and whether a dendrogram based on ecological similarity resembles most closely a dendrogram based on arrangement of the species by rarity and/or phylogeny (Fig. 7.1). Secondly, I map individual ecological traits of the species onto the hypothesized phylogenetic relationship of these species (based on Vitt 1984, Vitt *et al.* 1998, Cox *et al.* 2000) to graphically depict the co-occurrence of traits and their correspondence to rarity and phylogeny.

Analysis of ecological similarity and trait occurrence.

Throughout this thesis I have asked the question: do rare and common species differ in their limitations. In this chapter, I change focus from species to traits and from limitations to local persistence. Here local persistence is the ability of a species to maintain its population at a site year after year. Limitations set the boundaries of species distributions, while traits pertaining to local persistence determine the variability in these distributions. Local persistence is partly a function of life history strategy, and all of my species are perennials. Although the data used here represents evidence only for short-term persistence, there is reason to argue that such measurements have relevance to longer-term persistence. Evidence of the longer-term persistence of the rare species at the study sites exists in the form of herbarium records of the species from these sites. In my analysis of traits relating to local persistence I include all eight factors measured that pertain to persistence at a site. These traits include intrinsic factors relating to capability for population stability and/or expansion and proxies for the two extrinsic factors, disturbance and competition. The eight ecological traits relating to local persistence analysed by UPGMA (unweighted-pair groups method analysis) were: *in situ* yield (ΦPSII), colony expansion (3 yrs), neighbor contact, disappeared colonies (3 yrs),

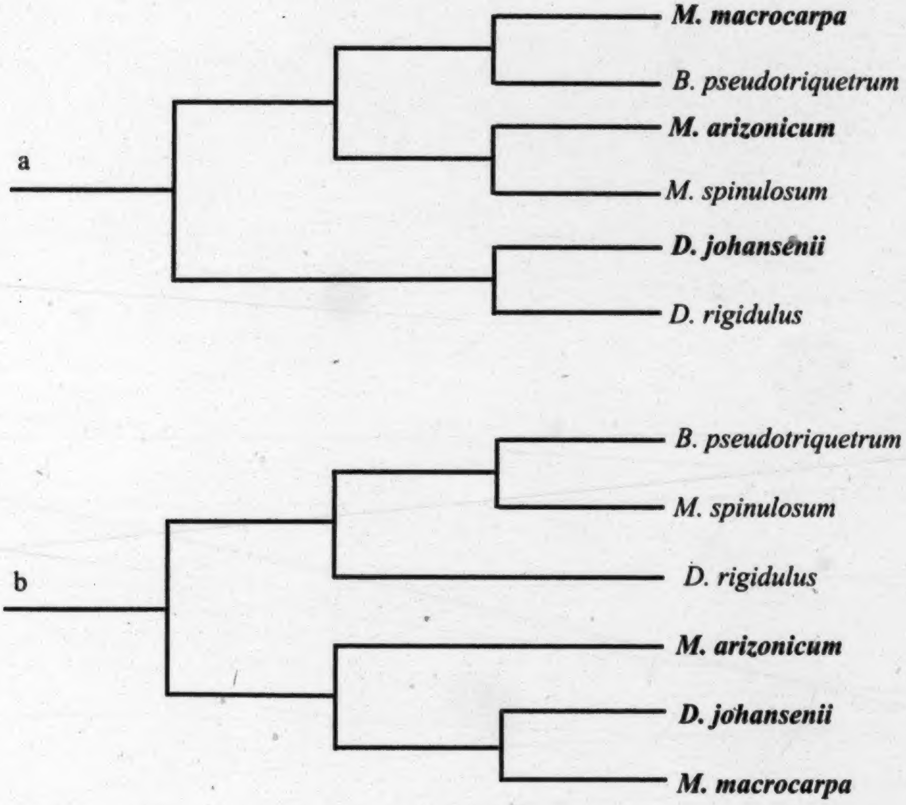
a
M. macrocarpa
B. pseudotriquetrum
M. arizonicum
M. spinulosum
D. johansenii
D. rigidulus
b
B. pseudotriquetrum
M. spinulosum
D. rigidulus
M. arizonicum
D. johansenii
M. macrocarpa

Figure 7.1. Representation of differences between a. dendrogram reflecting species phylogeny and b. dendrogram reflecting species rarity with the rare species in bold. The most important difference is the first dichotomy, which differentiates the diplolepideous mosses from the haplolepideous mosses (a) or differentiates rare species from the common species (b). Note that the more general term dendrogram is used in this chapter, although the dendrogram based on phylogeny could more specifically be called a cladogram.

neighbor encounters lost, regeneration ability (4 mos), local abundance, and sporophyte frequency. All measurements except yield were recorded as percentages. Data for the first seven ecological measurements are from Chapter 6, and those for local abundance and sporophyte frequency are from Chapter 2. The means of these traits for each species were used and data was standardized and centered for each trait using the equations in Jongman *et al.* (1995, pg. 20-21). The UPGMA (i.e., group averaging) cluster analysis was run using Euclidean distance in PC-ORD 4.0. UPGMA was chosen as the clustering method because of its known fidelity to the original similarity matrix (Sneath & Sokal 1973). However, nearest and furthest neighbor clustering methods also yielded the same dendrogram.

To address the question of trait co-occurrence, the eight traits previously analysed plus six additional traits were scored for three pairs of closely related rare and common moss species. As many traits as possible were included in this mapping exercise and trait selection was contingent only upon having a complete data set for the trait, i.e. data for all six species. Trait scores are described in Table 7.1 and scoring of species is presented in Appendix B. A hypothetical dendrogram (Fig. 7.1a) was constructed based on the higher order relationships suggested by Vitt *et al.* (1998) with the first division representing fundamentally different peristome development patterns, the diplolepideous (Bryum-type) and haplolepideous (Dicranum-type) clades (Fig. 7.1a). Generic relationships for *Mnium*, *Bryum* and *Mielichhoferia macrocarpa* follow Cox *et al.* (2000). Specific relationships of the species pairs are detailed in Chapter 2. The fourteen traits were then mapped onto this dendrogram to visualize the occurrence of the traits on branches of the dendrogram using MacClade 3.0 (Maddison & Maddison 1992).

Ecological similarity.

Rare and common species clustered separately, though the rare species were more ecologically similar to one another than the common species (Fig. 7.2, note similarity to Fig. 7.1b). The overall ecological similarity of the rare species (Fig. 7.2) indicates that these species may have similar strategies such as high growth rates to promote their local persistence (Chpt. 6). The two species of *Mnium* were the closest species ecologically and they were the only pair to group by phylogeny (Fig. 7.2). The ecological affinity of

Table 7.1. Ecological characters scored for six study species summarizing the traits, their character states, and the chapter source for the data. Species scorings are given in Appendix B.

Ecological character	Character states	Chapter source
1. Local abundance	0 – low (<0.001% cover), 1 – medium (<0.05% cover), 2 – high (> 0.05% cover)	Chapter 2 (Table 2.2)
2. Environmental breadth	0 – narrower than pair sp., 1 – same as pair sp., 2 – wider than pair sp.	Chapter 2 (Table 2.7)
3. Sporophyte frequency	0 – infrequent, 1 - frequent	Chapter 2 (Table 2.8) Chapter 5 (Table 5.7)
4. Asexual specialization	0 – absent, 1 - present	Chapter 2 (Table 2.9)
5. Substrate restriction	0 – absent, 1 - present	Chapter 3 (Fig. 3.3) Chapter 4
6. Establishment limitation	0 – absent, 1 – present	Chapter 6 (Figs. 6.1-3)
7. Physiological tolerance restriction	0 – absent, 1 – present	Chapters 3, 5 & 6
8. Short-term desiccation tolerance	0 – low, 1 – high	Chapter 5 (Table 5.2, Fig. 5.5)
9. Long-term desiccation tolerance	0 – low, 1 – high	Chapter 5 (Fig. 5.6)
10. Colony expansion	0 – low (<30%), 1 – medium (30-50%), 2 – high (>50%)	Chapter 6 (Fig. 6.5)
11. *In situ* yield (Φ PSII)	0 – low (<0.55), 1 – medium (0.55-0.65), 2 – high (>0.65)	Chapter 6 (Fig. 6.6)
12. Colony disturbance	0 – low (<30%), 1 – medium (30-50%), 2 – high (>50%)	Chapter 6 (Fig. 6.8)
13. Neighbor contact	0 – low (<30%), 1 – medium (30-50%), 2 – high (>50%)	Chapter 6 (Fig. 6.9)
14. Contact outcome	based on category with highest percent of colonies: 0 – loss, 1 – tie, 2 – win	Chapter 6 (Fig. 6.9)

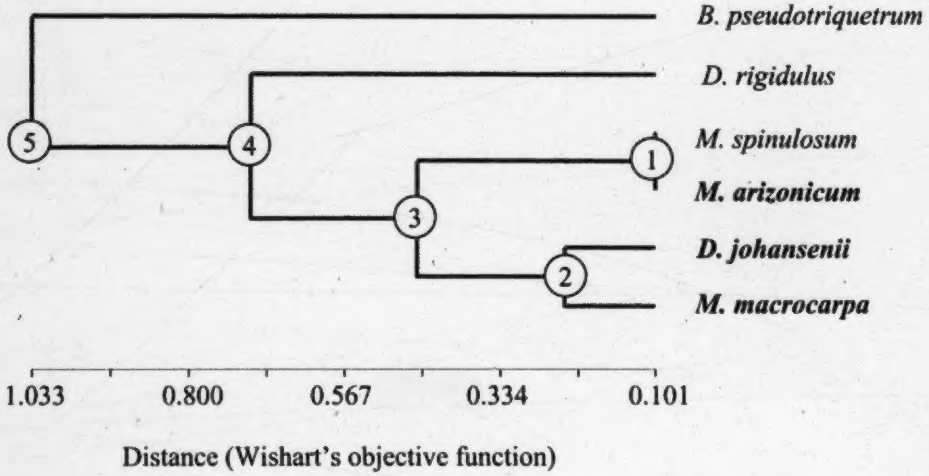
B. pseudotriquetrum
D. rigidulus
M. spinulosum
M. arizonicum
D. johansenii
M. macrocarpa
5
4
3
2
1
1.033
0.800
0.567
0.334
0.101
Distance (Wishart's objective function)

Figure 7.2. UPGMA dendrogram showing species similarity for nine ecological traits relating to local persistence: *in situ* yield (ΦPSII), colony expansion (3 yrs), neighbor contact, disappeared colonies (3 yrs), neighbor encounters lost, regeneration ability (4 mos), fragment disappearance (4 mos), local abundance, and sporophyte frequency. Numbers at the dendrogram nodes represent the order of group joining and are referred to in the text summary. Rare species are in bold.

the *Mnium* species agrees with Hedderson and Longton (1996) who concluded life history traits in the Polytrichales, Funariales and Pottiales were conserved at the generic level. Similarly, Hedenäs and Kooijman (1996) were able to resolve generic relationships in the Amblystegiaceae by including habitat data in their cladogram. The lack of strong generic clustering in this study is partially explained by the focus on function rather than morphology. For example, the two rare but morphologically very different species, *Didymodon johansenii* and *M. macrocarpa* (Table 7.2, Fig. 7.2, node 2) clustered together because these two rare species share high *in situ* yield (ΦPSII), low neighbor contact, low regeneration from gametophyte fragments, and high sporophyte frequency (Chpts. 2 & 6). In addition, they also share similar geographic distributions and substrate restrictions that are linked to their low establishment from fragments (Chpts. 3, 4, 6).

In contrast to the ecological similarity of the rare species, the relative dissimilarity of the common species indicates that there are many strategies for being common. This result contradicts the implications of Rabinowitz's (1981) classification indicating that there is only one type of common species and seven types of rare species. This study demonstrates that while there may be many types of rare species (*sensu* Rabinowitz 1981), these types may be functionally very similar in their local ecology. However, the common species tend to be functionally dissimilar in their ecology and this at least partially relates to their being limited in later life stages. Habitat differences, such as the relative importance of disturbance and neighbor contact, were more directly related to ecological differences for the common species. For instance, *Bryum pseudotriquetrum* appears to be a relatively strong competitor with the lowest number of losses and greatest number of wins in neighbor encounters (Chpt. 6). *Didymodon rigidulus* is a weak competitor that experiences high colony disturbance and has few neighbor encounters (Chpt. 6). *Bryum pseudotriquetrum* sites do experience occasional flood disturbance that results in moderate disappearance of colonies (Chpt. 6), and may be important in dispersal (Chpt. 5). The low *in situ* yield and colony expansion for both *B. pseudotriquetrum* and *D. rigidulus* probably resulted from photoinhibition in their relatively high light habitats (Chpt. 5). *Mnium spinulosum* likely clustered with the three

Table 7.2. Comparison of species similarity by number of shared traits out of fourteen scored (below diagonal) and Euclidean distance matrix for nine continuous traits relating to local persistence (above diagonal). Co-occurrence of scored traits are shown in Figures 7.2-4, and a dendrogram summarizing species similarity in traits relating to local persistence is shown in Figure 7.5.

	Mmac	Bpse	**Djoh**	Drig	**Mari**	Mspi
Mmac	____	0.7064	0.2707	0.5536	0.3517	0.4637
Bpse	3	____	0.7968	0.6778	0.4682	0.6455
Djoh	4	4	____	0.3739	0.4517	0.4931
Drig	7	4	6	____	0.4488	0.6239
Mari	2	6	10	6	____	0.2011
Mspi	4	6	7	5	9	____

rare species because of its ecological similarity to *M. arizonicum* (Table 7.2, Fig. 7.2). The key to *M. spinulosum*'s circumboreal distribution probably results from its prolific spore production and ability to pre-empt suitable habitat space. Some data indicating the ability of *M. spinulosum* to regenerate efficiently from spores comes from a comparison of spore germination on agar in the field for *M. spinulosum* and *M. macrocarpa*. *Mnium spinulosum* had higher spore germination (88.3±3.0%) than *M. macrocarpa* (55.7±4.1%) (Mann-Whitney U, $Z = -5.325$, $p < 0.001$, unpubl. data).

The ecological dissimilarity of the common species may also be partly reflected in their differing physiological limitations. That is, *B. pseudotriquetrum* lacks even short-term desiccation tolerance (Chpt. 5), *D. rigidulus* is restricted to calcareous soil with frequent small scale disturbance (Chpt. 3 & 6), and *M. spinulosum* is intolerant of high light levels (Chpt. 5). The limitations of the common species are apparent in the match between their physiology and the types of habitats that they occupy, and this was not the case for the rare species (Chpts. 5 & 6). Therefore, the explanatory power of habitat differences for the ecological dissimilarity of common species does not apply to the rare species, even though the rare species also differed in their habitats. This strengthens the conclusion that their ecological similarity can be attributed to their rarity.

Co-occurrence of ecological traits.

The co-occurrence of ecological traits along phylogenetic lines has been found in many taxonomic groups including mosses (Hedderson & Longton 1996), fishes (Pyron 1999) and bats (Arita 1993). The co-occurrence of traits on a phylogenetic tree is often interpreted with caution as suggesting co-adaptation of those traits (Hedderson & Longton 1996, Pyron 1999). The ecological traits examined here include both species traits and habitat traits. There were three clusters of co-occurring ecological traits (Figs. 7.3-5). The co-occurrence of habitat traits such as high neighbor contact and low colony disappearance agrees with the logic underlying the plant strategy theory of Grime (1979). In addition, habitats with high neighbor contact and low disturbance were associated with the species that are not substrate specific and have no limitations during establishment, namely, *B. pseudotriquetrum*, *M. arizonicum* and *M. spinulosum* (Fig. 7.3). Does substrate specificity represent an avenue by which bryophytes avoid competition? In any

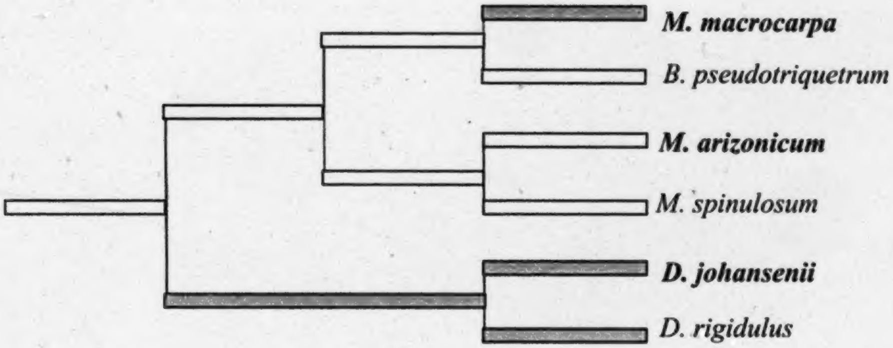
M. macrocarpa
B. pseudotriquetrum
M. arizonicum
M. spinulosum
D. johansenii
D. rigidulus

Figure 7.3. Colony disappearance, neighbor encounter, establishment ability and substrate restriction. Tracing of ecological traits on a dendrogram representing hypothesized evolutionary relationships of the six study species. White branch traits are: low disappearance of colonies, high neighbor contact, lack of establishment limitation and no substrate restriction. Substrate specificity is thought to be a derived trait within the Bryales (Vitt 1984), and all three species lacking substrate specificity occur on soil or humus. Gray branches have higher colony disturbance, lower neighbor contact, and substrate restrictions that correspond with establishment limitations.

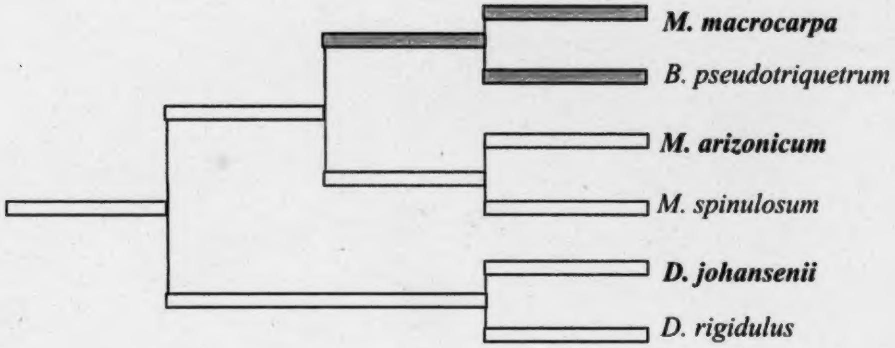
M. macrocarpa
B. pseudotriquetrum
M. arizonicum
M. spinulosum
D. johansenii
D. rigidulus

Figure 7.4. Local abundance and neighbor encounter outcome. Dendrogram representing relationships among six moss species showing characters restricted to members of the family Bryaceae in this study. Gray branches represent the traits of high local abundance and low loss of neighbor encounters. The polarity of these characters within the Bryales is not clear, but their co-occurrence along phylogenetic lines is of ecological interest. White branches represent character states of low to medium local abundance and high loss of neighbor encounters.

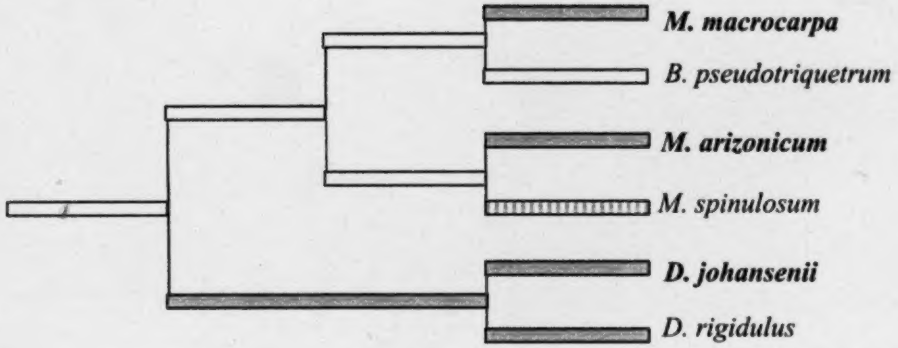
M. macrocarpa
B. pseudotriquetrum
M. arizonicum
M. spinulosum
D. johansenii
D. rigidulus

Figure 7.5. Short-term and long-term desiccation tolerance. The co-occurrence of ecological traits on a dendrogram representing the current phylogenetic hypothesis for six taxa in the Bryales. Gray branches correspond with possession of both short- and long-term desiccation tolerance (i.e, long-term propagule viability in air storage). *Mnium spinulosum* possessed short- but not long-term desiccation tolerance indicated by a striped branch. Desiccation tolerance is thought to be a derived trait within the Bryales (Vitt 1984). White branches denote lack of these two traits. Rare species are in bold and all three possess desiccation tolerance and specialization for asexual reproduction.

case, the link between low establishment and substrate restriction found for the other three species in this study implies that such avoidance may have costs (Fig. 7.3, Chpts. 3, 4 & 6). That is, these three species may be specialized to grow where other moss species cannot, but even they have difficulty in establishing in these microsites.

The co-occurrence of ability to tie or win in neighbor encounters and the ability to achieve high local abundance varied along taxonomic lines (Fig. 7.4). Arita (1993) also found the tendency for local abundance to vary with taxonomy in bats and this variation related to differences in trophic category with insectivorous and carnivorous bats having lower local abundance. For *M. macrocarpa* and *B. pseudotriquetrum*, ability to achieve high local abundance may also relate to resource availability in that these two species grow in habitats with secondary sources of moisture during the growing season, while the other four species rely solely on rainfall (Chpt. 2). Long-term propagule viability and short-term colony desiccation tolerance were possessed by all three rare species and only one common species (Fig. 7.5; Chpt. 5). For three of these species, *M. arizonicum*, *D. johansenii* and *D. rigidulus*, long-term propagule desiccation tolerance and adaptations for asexual reproduction also coincided, and these three traits may be adaptively related (Chpt. 5).

Of the six species, *M. macrocarpa, D. johansenii* and *D. rigidulus* most often possessed attributes posited by Vitt (1984) as derived within the mosses, namely desiccation tolerance and habitat specificity (Figs. 7.3, 7.5). Prior studies examining the relationship of ecologically related traits to taxonomy in mosses have found taxonomy to explain most of the variation, although, in general, gametophyte characters influencing water relations were most closely correlated with environmental parameters (Hedderson & Longton 1996, Hedenäs 1999). In a comparison of phylogenetic and environmental influence on character states, Hedenäs (1999) could best explain character state variation in pleurocarpous mosses at the species level using taxonomic position rather than environmental variables. The lack of obvious phylogenetic influence on species ecological traits found here together with the results of Hedenäs (1999) implies that morphological characters have a large historical component (i.e., time lag) and do not necessarily reflect functional differences between taxa.

In summary, the ecological differences and similarities between these six moss species suggests a need to reconsider the functional significance of the seven widely used rarity categories of Rabinowitz (1981). Here the common species were shown to be more ecologically diverse than the rare species. A rarity continuum for the species (presented in Chapter 2) coincided with an intriguing split in ecological traits. The three species closest to the rare end of the continuum were all substrate specific and had lower neighbor contact, higher colony disappearance and lower regeneration than the other three species. The co-occurrence of these traits raises interesting hypotheses concerning the relationship between habitat specificity and the relative importance of competition and disturbance for these mosses and plants in general.

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Chapter 8: General discussion and conclusions

The study of rarity dates back at least to Darwin (1859) and his contemporaries and is currently associated with the field of conservation biology (e.g., Soulé 1986, Arita *et al.* 1990). Within conservation biology, rarity studies are often split between studies of population genetic focusing on "small population problems" and species origins, and autecological studies focusing on "declining population problems" and proximate limitations of rare species (Caughley 1984, Schemske *et al.* 1994). Recent reviews have additionally noted an imbalance in the quantity of genetic versus ecological data for rare species (Gitzendanner & Soltis 2000, Asquith 2001), and several studies have called for more autecological data on rare species (Brussard 1990, Lahti *et al.* 1991, Arita 1993, Gaston & Kunin 1997, Bevill & Louda 1999). The need for the series of autecological studies in this thesis is further supported by the paucity of such data for bryophytes in general (Söderström & Herben 1997), and for rare bryophyte species in particular (Chpt. 1).

In this comparative study of three rare and three common moss species, the rare species were limited during the earlier part of their life cycle, dispersal and establishment. These early limitations may explain the poor match between colony physiology and occupied habitat for the rare species. In contrast, the common species appear better at filling "suitable" space and tended to have a good match between habitat and adult physiology. This study therefore suggests a new rarity hypothesis: rare are limited during earlier parts of their life cycle than common species. In terms of local persistence (i.e., ability to maintain local population), there were ecological differences between the rare and common species with the rare species more ecologically similar to one another than were the common species (Chpt. 7). Ecological similarity could not be attributed to similarities in phylogeny or habitat type among the rare species. I include a caveat here that two other traits shared by the rare species in this study were smaller size and occupation of cooler, darker habitats relative to their common congeners (Chpt. 2). Whether these two traits are a cause or consequence of rarity is unknown; however, both of these traits influence ability for local persistence.

For the rare species, the difficulty of establishing new populations coupled with ability for local persistence provides a sound ecological argument as to why habitat preservation is so vital. When management is required due to habitat destruction, this study indicated that establishment of new populations will be most successful via propagule testing of habitats rather than by adult transplants. As shown here, adult transplants may be able to survive, at least in the short-term, in habitats where they are unable to establish. Therefore even if they persisted in the long-term, they would still probably fail to produce viable new populations.

The classification of naturally rare species proposed by Fiedler and Ahouse (1992) received strong support from this study while that of Rabinowitz (1981) did not. Traits that corresponded well with differences in the ecology of rare species in this study were geographic distribution pattern and hypothesized species age in agreement with the classification of Fiedler and Ahouse (1992). The utility of Rabinowitz's (1981) inclusion of habitat specificity as a factor differentiating rare and common species is questionable for bryophytes (Chpts. 1 & 3). Both rare and common species were habitat specific (i.e., relatively narrower habitat breadth than congener), and the common species that was habitat specific occurred in a widespread habitat (Chpts. 2 & 3). If we wish to create a classification of rarity for bryophytes, then the parameters of geographic distribution pattern and global frequency may create the most ecologically meaningful groupings. In addition, a relative continuum approach such as that created for the six species using rank sums in Chapter 2 may be more realistic than a strict delimitation of categories (as in Rabinowitz (1981)). Future research on the relationship between local abundance and range size should consider not only phylogenetic, but also phytogeographic history of the species. For instance, are other endemic mosses more similar in ecology to *M. arizonicum* than to their common congeners, and do these species tend to have poor dispersal ability?

Once we have a classification that relates to ecologically relevant groups of rare species, then we should ask: how do existing rarity hypotheses relate to these groupings and do different hypotheses pertain to different types of rarity? The results of this thesis present a preliminary "yes" to the latter question. The two widely disjunct rare species both lent partial support to the niche breadth hypothesis of Brown (1984, 1995) and the resource availability hypothesis of Hanski *et al.* (1993), with the important caveat that these restrictions are imposed in the regeneration niche (Grubb 1977). Note that these two hypotheses could not be quantitatively distinguished in this study because to do so requires quantification of resource availability and limitation on the landscape. O'Connor's (1987) habitat selection hypothesis may also apply to the disjunct species, although further experiments on biotic interactions during establishment are required to fully evaluate his hypothesis. In contrast, the endemic distribution of the third rare seemed best explained by Hanski's (1991) metapopulation hypothesis. That is, the habitat restriction of *M. arizonicum* did not relate to substrate, environment, establishment or competitive restrictions within the scope of this study, and most likely this species is dispersal limited.

In addition to contributing to rarity theory, this thesis draws several conclusions relevant to plant ecology in general. The first of these relates to substrate specificity. Substrate restrictions were linked to the establishment stage. These restrictions were mechanistically related to moss physiology and substrate physical properties. Physiological substrate restrictions were most profound for the two calcicole species in the study (Chpt. 3). Physically based substrate limitation (i.e., the need for mitigation of disturbance) was concluded for the one species, *D. johansenii* that occupied substrates where adherence is difficult (Chpt. 4).

Secondly, habitat restrictions that are suspected as physiologically based from known patterns of habitat occupation must always be confirmed experimentally because the reasons for habitat specificity patterns are varied. As a consequence, non-experimental studies demonstrating correspondence between habitat breadth or specificity and rarity (or any other species trait) should be cautious about claiming support for these hypotheses since they require differentiation between the causes of habitat specificity (Chpts. 1 & 6). For instance, the third rare species, *M. arizonicum,* has been described as habitat specific, but was not physiologically restricted to the sub-alpine habitats where it most frequently occurs. Correlation between reported habitat breadth and other traits are of doubtful functional significance for management because they group together species with very different ecological restrictions.

Thirdly, dispersal and establishment limitations are functionally separate for gametophyte fragments, i.e., the species with high fragment viability did not necessarily have high establishment in the field and visa versa (Chpt. 5; see *M. macrocarpa* and *M. spinulosum*, in particular). This still needs to be tested for spores; however, the current evidence argues for the inclusion of two separate parameters for dispersal and establishment ability in metapopulation models (Söderström & Herben 1997). Fragment desiccation tolerance corresponded both to colony desiccation tolerance and to specialization for fragment detachment from the colony (Chpt. 5 & 7). The coincidence of desiccation tolerance and habitat restriction observed in this study is in agreement with the hypothesis that evolution of desiccation tolerance is key to the diversity of substrates that bryophytes now colonize (Vitt 1984, Proctor 2001).

The many new methods or new applications of methods presented in this thesis may prove useful for future studies. For instance, testing the degree of overlap between fundamental and realized niches through eco-physiological experiments presents a novel complement to the widely used reciprocal transplant method for testing theories on niche relationships (Chpts. 3, 5 & 6). Much basic demographic data remains to be collected for bryophytes and the colony assessments used here to quantify colony expansion and disappearance can contribute to our understanding of bryophyte demography in habitats with different disturbance regimes (Chpt. 6). These types of demographic data are needed for building metapopulation models that may then be used for conservation decisions (Söderström & Herben 1997). Rare bryophyte reintroduction efforts and establishment of populations in botanical gardens may benefit from the methods developed here for establishment and transplantation of rare mosses occurring on soil, rock and logs. These methods also allow distinctions to be made between two functionally different establishment restrictions, physiological and physical (Chpts. 3, 4 & 6). This distinction may be especially important in bryophyte regeneration studies, since many species exhibit substrate specificity and grow on substrates difficult for propagule adherence (e.g., rocks and logs).

In conclusion, this study of six moss species has been able to distinguish between the relative importance of several ecological factors, namely disturbance, habitat, propagule viability, establishment, neighbor interaction and colony physiology. The results from these species suggest a new rarity hypothesis: rare species are limited earlier in their life cycles than common species. This early limitation results in an apparent mismatch between colony physiology and habitat, and may indicate that rare species are not filling many suitable habitats or that the habitat requirements during establishment are more specific than in later colony stages. Some key areas not well explored in this thesis include competition during the establishment stage, spore production and dispersal, and the potential role of sporophyte herbivory in dispersal limitation. Comparative autecological studies of rare and common species, remain the best means of testing and generating hypotheses on rarity. Despite their time requirements and low number of species comparisons, they have the power to distinguish between limiting mechanisms; a capability that is lacking in the many comparative studies based on literature surveys.

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Appendix A: Summary of autecological studies on rare vascular species used in literature review in Chapter 1.

Table A.1. Autecological studies on rare plant species summarized for species limitations. Studies are arranged alphabetically by family, genus and species. Names of species considered rare in the study are bolded. Range description for the species gives a proxy of rarity type. Methods used in the articles are abbreviated: environmental measurements (env), experimental (exp), monitoring (mon), survey (sur), and review (rev). Limitations considered and found are numbered to coincide with Table 1.5: 1. historical, 2. disturbance, 3. dispersal, 4. establishment, 5. competition, 6. differential mortality, 7.reproductive biology, and 8. habitat specificity. Studies where considered limitations are not stated are entered as "none". Likewise, studies where no limitation was found are entered as "none". Limitations that were mentioned, but were not addressed in the results of the paper are not included. Citations for studies that compared rare and common species are in bold. For species with more than one study, the studies were separated when they had been conducted by different authors on different populations of the species. References for this table are included in the literature cited section for Chapter 1.

Family **Study species**	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Alismataceae					
Luronium natans	anth, Europe	env, exp	8	none	Greulich *et al.* 2000
Sagittaria fasiculata	ende, aquatic, N & S Carolina	exp,mon	5,7,8	5,8	Newberry 1991
Apiaceae					
Eryngium cuneifolium	ende , Florida scrub	sur	2,5,8	2,5	Menges & Kimmich 1996
Lomatium bradshawii	ende, OR & WA	exp	2 (fire)	none	Pendergrass *et al.* 1999
Peucedanum palustre	rang, Britain	rev	3,4,5,6,7,8	3,4	Harvey & Meredith 1981
Araliaceae					
Panax quinquefolium	anth rarity	mon	6,7	none	Carpenter & Cottam 1982
		mon	4,7	4	Charron & Gagnon 1991
		mon	4,7	7	Lewis & Zenger 1982
Araucariaceae					
Wollemia nobilis	paleoende , Australia	mon	4,7	4	Offord *et al.* 1999

Table A.1. continued

Family Study species	Rarity/Range description	Method	Consider	Support	Study
Asclepiadaceae					
Asclepias meadii	ende, tallgrass prairie, N. America	env,exp, sur	2,4,5,8	2,4,5,8	Bowles *et al.*1998
		mon	2,7	none	Kettle *et al.* 2000
Asclepias quadrifolia, A. syriaca	NE rang, Vt	mon	7	7	**Cabin *et al.* 1991**
Asteraceae					
Argyroxiphium sandwicense	ende, Mauna Kea, Hawaii	exp	4,6,7,8	6	Walker & Powell 1999
Arnica montana	s. rang, the Netherlands	exp	6	6	Bruelheide & Scheidel 1999
		exp	3	3	Strykstra *et al.* 1998
Aster curtus	ende, prairie, Pacific NW	mon	4,7	4	Clampitt 1987
		exp	7	none	Giblin & Hamilton 1999
Aster kantoensis	ende, river gravel bars, Japan	exp	4,7	4	Inoue *et al.* 1998
Aster laurentianus	ende, salt marshes & lagoons, St. Lawrence estuary	exp	8	8	Houle & Belleau 2000
Boltonia decurrens	ende, Illinois River valley	sur	8	8	Smith *et al.* 1993
Carlina onopordifolia	anth rarity, Europe	exp	8	none	Poznanska 1989
Carlina vulgaris	rang locally rare, England	mon, exp	5,6,7,8	6,7	Greig-Smith & Sagar 1981
Cirsium eriophorum, C. vulgare		exp	4,7,8	4	**Tofts & Silvertown 2001**
Cirisium pitcheri	ende, sand dunes, Great Lks	mon, exp	4	2	Hamzé & Jolls 2000
		exp	6	6	Bevill *et al.* 1999
Echinacea tennesseensis, E. angustifolia	ende, cedar glades, Tennessee	rev	n/a	1,3	**Baskin *et al.* 1997**
		exp	8	none	**Baskauf & Eickmeier 1994**
Echinacea tennesseensis, E. angustifolia, E. pallida		exp	5	none	**Snyder *et al.* 1994**
Erigeron kachinensis	ende, canyons, Utah & Colorado	mon	none	2	Allphin & Harper 1997
Eupatorium resinosum, E. perfoliatum	ende, pine barren ,NJ – Del.	mon, exp	2,4,7	2,7	**Byers & Meagher 1997**
		mon	7	7	**Byers 1995**
Helenium virginicum	ende, seasonal sinkhole ponds, VA	sur, env	8	8	Knox 1997
		exp	7	7	Messmore & Knox 1997
Helianthus paradoxus	ende, inland saline marshes, NM, TX	exp	5,6	5	Bush & van Auken 1997

Table A.1. continued

Family **Study species**	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Helipterum albicans	ende, Tasmania	exp	4,5.	4,5	Gilfedder & Kirkpatrick 1993
Hymenoxys acaulis* var. *glabra	ende, Great lakes, N. America	exp	7	7	DeMauro 1993
Hypochoersis radicata, Cymbonotus lawsonianus, ***Microseris lanceolata***	anth, declining sp. Australia	sur	2,8	2	**McIntyre 1995**
Pulicaria vulgaris & Lactuca saligna	rang	rev	2,4,8	2,4	Prince & Hare 1981
Senecio integrifolius	anth, declining sp, Sweden	exp	7	none.	Widen 1993
Solidago shortii	ende, cedar glades, Kentucky	env	8	none	Buchele *et al.* 1989
		mon	3,7	none	Buchele *et al.* 1991
		rev, exp	2,4,5,7,8	2,4,5,8	Walck *et al.* 1999a,b,c,d
Solidago shortii, S. altissima		rev	n/a	3,5	**Baskin *et al.* 1997**
Boraginaceae					
Echium acanthocarpum	ende, Canary Islands	exp	3,4,5	3,5	Marrero-Gomez *et al.* 2000
Myosotis oreophila, M. pulvinaris	ende, high-alpine, S. Island, New Zealand	mon	6,7	1	**Stanley *et al.* 1998**
Brassicaceae					
Erysiumum capitatum* ssp. *angustatum	ende, Contra Costa Co., CA	exp, mon	4,6,8	8	Pavlik & Manning 1993
Lepidium sisymbrioides	ende, New Zealand, 3 ssp.	exp, mon	4,6,7,8	8	Allen 1998
Lesquerella lyrata	ende, N. Alabama	exp	4	none	Baskin & Baskin 2000
Bruniaceae					
Staavia dodii	ende, SW cape of S. Africa	sur	2,4,8	2,8	Moll & Gubb 1981
Cactaceae					
Ancistrocactus tobushii	ende, Edwards Plateau, TX	sur	8	none	Sutton *et al.* 1997
Peniocereus striatus	ende, Sonoran Desert, Mexico, US	sur	7,8	1,7,8	Suzan *et al.* 1994
Caryophyllaceae					
Silene douglasii var oraria	ende, west coastal prairies, Oregon	mon	7	7	Brown & Kephart 1999
		mon	4,5,8	5,8	Kephart & Paladino 1997

Table A.1. continued

Family Study species	Rarity/Range description	Method	Consider	Support	Study
Silene regia	ende,midwest prairie, N.America	mon	2,4,7	2,4	Menges & Dolan 1998
		exp,mon	2,4,5,7	2,4	Menges 1995
Silene spaldingii	ende to NW, Wa, Or, Id, Mt	exp	2,4	1,2,4	Lesica 1999
Clusiaceae					
Hypericum cumulicola	ende, Florida scrub	sur	2,5	2,5	Quintana-Ascendio & Morales-Hernandez 1997
Convolvulaceae					
Calystegia collina	ende, serpentine rock, Coast Range, N. CA		7	7	Wolf *et al.* 2000
Crassulaceae					
Diamorpha smallii	ende, granite outcrops, SE US	exp	5,7	5,7	Clay & Shaw 1981
Sedum integrifolium ssp. leedyi	ende, N. America disj, MN, NY, CO, NM	exp, sur	4,7	none	Olfelt *et al.*1998
Cyperaceae					
Scirpus longii	Disj, N. of range, Nova Scotia	sur	8	(5)	Hill & Johansson 1992
Diapensiaceae					
Shortia galacifolia	paleoende	sur	2	2	Vivian 1967
Epacridaceae					
Epacris stuartii	ende, SE Tasmania	exp	4	2(fire)	Keith 1997
Eriocaulaceae					
Eriocaulon kornickianum	ende, western N. America	mon,sur	2,4,5,6,7,8	2,5,7,8	Watson *et al.* 1994
Euphorbiaceae					
Jatropha standleyi & J. chamelensis	ende, Chamela Bay, Mexico	mon	3,7	7	**Pirie *et al.* 2000**
Fabaceae					
Astragalus australis* var. *olympicus	ende, Olympic Mts., Washington	mon	6,7	6	Kaye 1999
Astragalus cremnophylax* var. *cremnophylax	ende, Grand Canyon	mon	2,3,4,6	2,3,4,6	Maschinski *et al.* 1997
Astragalus lentiginosus var. micans	ende, sand dunes, Eureka Valley, CA	env, exp	(5),8	(5),8	**Pavlik 1980**
Astragalus linifolius, A. osterhouti, *A. lonchocarpus, A. pattersoni*	endes, Colorado	exp, mon	7	7	**Karron 1987**
Astragalus scaphoides	ende, central ID, MT	mon	4,6,7	none	Lesica 1995

Table A.1. continued

Family **Study species**	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Clianthus puniceus	ende, New Zealand, declining	mon, sur	3,4,6,7,8	3,6,8	Shaw & Burns 1997
Ebenus armitagei	ende, west Meditteranean coast, Egypt & Libya	mon	6,7	6	Hegazy & Eesa 1991
Lupinus guadalupensis	ende, islands, CA, Mexico	exp, mon	3,6,8	3,6	Helenurm 1998
Thermopsis macrophylla* var. *agnina	ende, chaparral, CA	mon	3,4,7	4	Borchert 1989
Vicia pisiformis, V. dumetorum	rang Sweden, European	exp	8	8	BlackSamuelson & Anderson 1997
Gentianaceae					
Gentiana cruciata	s. rang, rare in the Netherlands	exp, mon	7	7	Petanidou *et al.* 1995
Gentiana pneumonanthe	s. rang, rare in Netherlands	exp	7	none	Petanidou et al 1995
			2,4,7	2,4	Rose *et al.* 1998
Gentianella germanica	anth "declining sp" Europe	mon, exp	2,3,4	2,3,4	Fischer & Matthies 1998
Iridaceae					
Iris lacustris	ende to Great Lakes	exp,mon	3,7	3	Planisek 1983
Juncaceae					
Juncus caesariensis	ende, boggy open habitats, NJ, MD & VA	sur	8	8	Strong & Sheridan 1991
Lamiaceae					
Acanthomintha duttonii	ende, serpentine rock, CA	exp, mon	7	none	Pavlik & Espeland 1998
Dicerandra frutescens	ende, Lake Wales Ridge, Florida scrub	sur	2,8	2(fire),8	Menges 1992
		mon	7	none	Deyrup & Menges 1997
Pogogyne abramsii	ende, vernal pools	exp	5,8	8	Bauder 1989
Lauraceae					
Lindera melissifolia	ende, SE US	mon	7 (3)	none (3)	Devall & Schiff 2001
Liliaceae					
Calochortus albus, ***C. coxii, C. howellii, C. obispoensis, C.pulchellus, C. tiburonensis, C. umpquanensis, C. westonii***	endes, serpentine rock, California	mon	7	7	**Fiedler 1987** **Fiedler *et al.* 1998**

Table. A.1. continued

Family **Study species**	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Erythronium grandiflorum **var.** ***candidum***, *E. grandiflorum* var. *grandiflorum*	ende, Pacific NW	mon, exp	7	none	Fritz-Sheridan 1988
Erythronium propullans *& E. albidum*	ende, SE Minnesota	mon	7,8	8	**Morley 1982**
		mon	7	7	**Banks 1980**
Helionas bullata	disj, S. Appalachians from eastern coastal plain	mon	6,7,8	6,8	Sutter 1984
Smilax rotundifolia	n. rang, Ontario, Canada	mon	7	7	Kevan *et al.* 1991
Limnanthaceae					
Floerkea proserpinacoides	n. rang, Quebec	Exp	3,8	3	McKenna & Houle 2000
Lobeliaceae					
Lobelia urens	N. rang, S. Britain	sur, env	1,2,8	1,2	Dinsdale *et al.* 1997
		mon, exp	4,8	4,8	Dinsdale *et al.* 2000
Malvaceae					
Iliamna corei*, I. rivularis*	ende, cedar glades, Tennessee	rev	n/a	1,2	**Baskin *et al.* 1997**
Sidalcea malvaeflora var elegans	ende, garry oak stands, Pacific NW, N. CA to S. OR	exp, mon	7	7	Dimling 1992
Myrtaceae					
Eucalyptus paliformis	ende, Australia	exp	5	5	Prober & Austin 1990
Eucalyptus paliformis & *E. fraxinoides*		exp	8	none	**Prober 1992**
Onagraceae					
Oenothera avita ssp. eurekensis	ende, sand dunes, Eureka Valley, CA	env, exp	(5),8	(5),8	**Pavlik 1980** (see other species in study)
Oenothera deltoides **ssp.** ***howelii***	ende, Contra Costa Co., CA	exp, mon	4,6,8	6	Pavlik & Manning 1993
Orchidaceae					
Coeglossum viride	anth rarity, holarctic-boreal	mon	4,7	1(landuse)	Willems & Melser 1998
Isotria medeoloides	anth rarity, E N. America	mon	7,8	none	Mehrhoff 1989
Isotria verticilliata ***& I. medeoloides***		mon	3,7	none	**Mehrhoff 1983**
Lepanthes caritensis	ende, Puerto Rico	mon,sur	7,8	7,8	Tremblay *et al.* 1998
Ophrys sphegodes	N. rang, British Ilses	mon	6	6	Hutchings 1987

Table A.1. continued

Family Study species	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Spiranthes diluvialis	ende, Utah & Colorado	exp,mon	7	7	Sipes & Tepedino 1994
Spiranthes spiralis	rang	exp	7	none	Willems & Lahtinen 1997
Plantaginaceae					
Plantago cordata	anth rarity, eastern N. America	mon	2,8	2,8	Bowles 1989
		mon,sur	2,3,7,8	2,3,8	Meagher *et al.* 1978
Poaceae					
Achnatherum lemmonii, A. thurberiana, A. occidentale, ***A,*** ***hendersonii***	ende, WA & OR	exp	5,7	5	**Robson & Maze 1995**
Agrostis hiemalis, Festuca paradoxa, Setaria geniculata, Sphenopholis obtusata, *Schizachyrium scoparium, Sporobolus heterolepis, Andropogon gerardii, Sorghastrum nutans*	spar N. Am prairie grasses	exp	3,4,5,6,7	6,7	**Rabinowitz & Rapp 1981, 1985** **Rabinowitz *et al.* 1984** **Rabinowitz *et al.* 1989**
Calamagrostis porteri* var. *insperata	ende, mid-West US (S. IL)	exp	7,8 (light)	7	Havens & Holland 1998
		env,mon	8	8	Bittner & Gibson 1998
Dichanthelium lanuginosum* var. *thermale	ende, geothermal springs, Sonoma Co., CA	exp	8	8	Pavlik & Enberg 2001, Pavlik 2001.
Swallenia alexandre	ende, sand dunes, Eureka Valley, CA	env, exp	(5),8	(5),8	**Pavlik 1980** (see other species in study)
Zizania texana	ende, San Marcos River, TX	exp	7	7	Power 1997
Polygonaceae					
Chorizanthe pungens* var. *hartwegiana	ende, Santa Cruz Mts, CA	exp	2,8	2	Kluse & Doak 1999
Dedeckera eurekensis	paleoende, Mojave Desert, CA	exp	6,7,8	7	Wiens *et al.* 1989
Polygonum cascadense	ende, W. Cascade Mts, Oregon	mon	7,8	8	Hickman 1975
Proteaceae					
Banksia goodii & B. gardneri	neoende, SW Australia	env,exp, mon	6,4,7,8	1,8	**Witkowski & Lamont 1997**
Banksia tricuspis	Australian ende	mon	7	none	Lamont & Van Leeuwen 1988
Orothamnus zeyheri	ende, Cape of S. Africa	mon, exp	2,6	2	Boucher 1981

Table A.1. continued

Family **Study species**	**Rarity/Range description**	**Method**	**Consider**	**Support**	**Study**
Rafflesiaceae					
***Rafflesia spp* (13)**	tropical endes	mon	7	7	Beaman *et al* 1988
Ranunculaceae					
Clematis hirsutissima* var. *arizonica	ende	exp	6,7,8	8	Maschinski *et al.* 1997
Clematis socialis	ende, Alabama	exp,mon	6,7,8	6,7,8	Timmerman-Erskine & Boyo 1999
Delphinium bolosii	ende	mon	7	7	Bosch *et al.* 1998
Ranunculus ophioglossifolius	anth, n. rang, England	mon, exp	2,4,8	2,4,8	Frost 1981
		mon, exp	4	4	Dring & Frost 1971
Rhamnaceae					
Spyridium microphyllum	ende, Tasmania	sur	2,3,5	2,3,5	Coates *et al* 1999
Spyridium obcordatum	ende, Tasmania	sur	2,3,5	3,5	Coates *et al.* 1999
Rosaceae					
Filipendula rubra	ende, N central US	mon	7	7	Aspinwall & Christian 1992
Potentilla robbinsiana	ende, Mt.	mon, exp	3,5	3,5	Graber 1980
Rutaceae					
Ptelea trifoliata	n. rang, Ontario	mon	3,7,8	3	Ambrose *et al.* 1985
Scrophulariaceae					
Amphianthus pusillus	ende, granite outcrop pools, SE	exp, mon	5,8	5	Hilton & Boyd 1996
Cordylanthus maritimus* ssp. *maritimus	anth rarity, CA, salt marshes	exp, mon	6,7,8	7	Parsons & Zelder 1997
			2,4,7,8	2,4,8	Zelder 1998
Pedicularis furbishiae	ende, St. John River, ME & NB	mon	7,8	8	Macior 1978,
		mon	2,8	2	Gawler *et al.* 1987
		sur	2,8	2,8	Menges 1990
		mon	2,4,7	2,4	Menges *et al.* 1986
Penstemon penlandii	ende, Colorado plateau	mon	7	none	Tepedino *et al.* 1999
Schwalbea americana	ende, long leaf pine stands, SE	exp, mon	2,7	2	Kirkman *et al.* 1998
Tomanthera auriculata	anth rarity, US	exp	4	none	Baskin *et al.* 1991
Stericuliaceae					
Fremontodendron decumbens	ende, chaparral, CA	mon	7	7	Boyd & Serafini 1992

Appendix B: Ecological character state scores for summarizing co-occurrence of traits by rarity and phylogeny in Chapter 7.

Table B.1. Character state scores for fourteen ecological characters described in Table 7.1 that were used to map character states onto a dendrogram representing the evolutionary relationship of the six study species based on relationships within the Bryales (Vitt 1984) (Figs. 7.2-4).

Ecological character	**Mmac**	Bpse	**Djoh**	Drig	**Mari**	Mspi
1. Local abundance	2	2	0	1	0	1
2. Environmental breadth	0	2	2	0	1	1
3. Sporophyte frequency	1	0	1	0	0	1
4. Asexual specialization	0	1	1	1	1	0
5. Substrate restriction	1	0	0	1	0	0
6. Establishment limitation	1	0	1	1	0	0
7. Physiological tolerance restriction	1	1	0	1	0	1
8. Short-term desiccation tolerance	1	0	1	1	1	1
9. Long-term desiccation tolerance	1	0	1	1	1	0
10. Colony expansion	2	0	1	0	1	1
11. *In situ* yield (Φ PSII)	2	0	1	1	1	1
12. Colony disturbance	1	0	0	2	0	0
13. Neighbor contact	0	2	1	0	2	2
14. Contact outcome	1	1	0	0	0	0